Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 34, No. 7, July 1977

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Fisheries and Environment Canada
Fisheries and Marine Service

Pêches et Environnement Canada
Service des pêches et de la mer

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Scientific Information and Publications Branch
Ottawa K1A 0E6

Direction de l'information et des publications scientifiques

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Journal of the Fisheries Research Board of Canada

Volume 34, No. 7, July 1977

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Public Health Aspects of "Codworm" Infection: A Review

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MARGOLIS, L. 1977. Public health aspects of "codworm" infection: a review. J. Fish. Res. Board Can. 34: 887–898.

Larvae of the nematode *Phocanema decipiens* (Ascaridida: Anisakidae), known as "codworm" in the vernacular, occur in the musculature of some cod and other marine fishes in both hemispheres, particularly in the temperate and polar climatic zones. The natural definitive hosts are Pinnipedia (seals, sea lions, walruses). For many years regarded incapable of surviving in man, recent reports from Japan indicate that in certain circumstances codworm larvae may temporarily invade the human gastric mucosa, producing clinical symptoms. Several nonclinical cases, in which the larval worms were expelled orally or in the feces of humans, have been reported from Canada (1), the USA (5), Greenland (1), and the U.K. (1). The source of human infections was raw, lightly marinated, or insufficiently cooked sea fish. The ability of codworm larvae to penetrate the stomach wall of other mammals has been demonstrated experimentally in rabbits, rats, dogs, and pigs. Natural infection of a dog in Hokkaido has been reported. For the human cases, information on age and sex of patients, specific source of infection, symptoms, and gross pathology are reviewed. The name applied to human infections and their diagnosis, treatment, prognosis, prevention, and public health implications are discussed. Cooking at 70°C for 7 min or 60°C for 10 min and freezing at −20°C for 24 h are lethal to codworm larvae in fish flesh, thus providing reliable methods for preventing human infections. Some comparisons are made with larval *Anisakis* infections in man and future research needs, particularly in relation to the public health question, are discussed.

MARGOLIS, L. 1977. Public health aspects of "codworm" infection: a review. J. Fish. Res. Board Can. 34: 887–898.

Les larves du nématode *Phocanema decipiens* (Ascaradida: Anisakidae) communément appelé « ver de morue » se trouvent dans la musculature de certaines morues et autres poissons de mer des deux hémisphères, en particulier dans les zones climatiques tempérées et polaires. Les hôtes définitifs naturels sont les Pinnipedia (phoques, lions de mer, morses). On a cru pendant de nombreuses années que le parasite ne pouvait survivre dans l'homme, mais de récents rapports en provenance du Japon indiquent que, dans certaines circonstances, les vers de morue peuvent

Printed in Canada (J4717)
Imprimé au Canada (J4717)

envahir temporairement la muqueuse gastrique de l'homme, causant des symptômes cliniques. On a signalé plusieurs cas non cliniques au Canada (1), aux E.-U. (5), au Groenland (1) et au R.-U. (1) dans lesquels des larves de vers avaient été expulsés par la bouche ou dans les excréments d'êtres humains. La source d'infections humaines est du poisson de mer cru, légèrement mariné ou insuffisamment cuit. L'aptitude des larves de vers de morue à traverser la paroi abdominale d'autres mammifères a été démontrée expérimentalement chez des lapins, des rats, des chiens et des cochons. On a signalé l'infection naturelle d'un chien à Hokkaidō. Pour ce qui est des cas humains, nous passons en revue l'information sur l'âge et le sexe des patients, la source spécifique d'infection, les symptômes et la pathologie macroscopique. Nous discutons du nom donné aux infections humaines, de leur diagnose, traitement, pronostics, prévention et implications vis-à-vis de la santé publique. La cuisson à 70°C pendant 7 min ou 60°C pendant 10 min et la congélation à −20°C pendant 28 h causent la mort des larves de vers de morue dans la chair du poisson, fournissant ainsi des méthodes fiables de prévention d'infections chez l'homme. Nous comparons quelques cas d'infections de l'homme par *Anisakis* larvaire et discutons des besoins futurs en recherche, en particulier en ce qui a trait au problème de la santé publique.

Received Feburary 4, 1976
Accepted March 9, 1977

Reçu le 4 février 1976
Accepté le 9 mars 1977

THE "codworm," as it is popularly known, is a parasitic roundworm (Nematoda) belonging to the family Anisakidae of the order Ascaridida. Its specific scientific name has undergone a number of changes over the past 50 yr. Once called *Ascaris decipiens*, it later became *Porrocaecum decipiens*, then *Terranova decipiens*, and most recently *Phocanema decipiens* (see Myers 1959, 1975). Authorities on nematode systematics agree that the generic name *Porrocaecum* should no longer be used for this nematode, but not as unanimous are opinions on its allocation to *Terranova* or *Phocanema*. Hence, both names may be found in current literature. In recent Japanese literature the larvae from fish have been referred to as *Terranova* sp. larva Type A (Koyama et al. 1969; Shiraki 1974).

Although found with varying prevalences and intensities of infection in many species of marine fishes, in northern waters the larvae occur most frequently in cod, the obvious reason for the vernacular name. To some extent its common name is a misnomer, for the sexually mature stage occurs in seals and their relatives (occasionally also in porpoises) and hence it might more appropriately be called the "seal-worm." At any rate it has been dubbed the "codworm" and so it shall remain.

During the course of its life, the codworm undergoes development or growth in three hosts. Following mating in the stomach and possibly intestine of its marine mammal host, eggs are passed in the feces and hatch in the sea as second stage larvae, having molted once within the egg (Scott 1955; Myers 1960). Subsequent development probably occurs in certain small crustaceans (Scott and Black 1960; McClelland and Ronald 1974) when the second stage larvae are ingested, and further development or growth takes place in fish that have eaten infected crustaceans. In the fish the worms usually locate in the musculature (less frequently in the body cavity) and they are considered to be in their third larval stage (Shimazu 1974). They are brownish or reddish brown and measure 9–58 mm in length (most commonly 25–50 mm) by 0.3–1.2 mm in maximum width (Martin 1921; Scott 1956; Templeman et al. 1957; Koyama et al. 1969). These larvae are capable of reestablishing in the muscles of predator fish that prey on smaller infected fish, such as cod on smelt (Scott 1954). When seals feed on infected fish, the worms establish in the stomach, where they molt twice (Shimazu 1974) (once according to Scott 1953) and grow to mature adults, ready to reproduce their kind again. Each female worm produces hundreds of thousands of eggs.

For many years codworm was regarded as incapable of developing or surviving in man and hence of no public health concern. Following the discovery in Holland in the mid-1950s and a few years later in Japan that a close relative of the codworm, larval *Anisakis simplex*, or "herring worm" in the vernacular, was responsible for an acute abdominal syndrome in man (see Oshima 1972 for a review), some attention was turned to the possible public health hazards of codworm. (*Anisakis simplex* also occurs in cod fillets, but generally in much lower numbers than *Phocanema decipiens* (Templeman et al. 1957; Rae 1972).)

But even before this turn of events, codworm was the subject of much research in Canada and elsewhere because its presence in cod fillets repelled the consumer, with consequent adverse effects on marketing. Much was learned of the occurrence, life history, and biology of this parasite before there was any concern for its possible public health implications (Martin 1921; Kahl 1939; Scott 1953, 1954, 1955, 1956; Scott and Martin 1957; Templeman et al. 1957; Scott and

Fisher 1958a, b; Grainger 1959; Scott and Black 1960; Myers 1960; Rae 1963, 1972).

Natural Occurrence of Codworm

In its adult stage *P. decipiens* is a ubiquitous parasite of Pinnipedia (seals, sea lions, walruses), being particularly common in the temperate and polar climatic zones (Delyamure 1955; Dailey and Brownell 1972; Margolis and Dailey 1972; Dailey 1975). The third stage larvae likewise are widely distributed in marine fishes from Atlantic, Pacific, Arctic, and Antarctic waters, especially where the pinniped definitive hosts abound. Bottom- and near-bottom-dwelling fishes in continental shelf waters are the most frequent hosts. Pelagic and open-ocean fishes are less commonly and often only occasionally infected.

There are many published reports of *Phocanema* larvae (as *Terranova*, *Porrocaecum*, or under an older name applied to larvae) in marine fishes, in most cases almost certainly *Phocanema decipiens*. Only a few will be mentioned or summarized here to provide examples of the numbers of species of fishes reported as intermediate hosts in various geographic regions. In the northern hemisphere, larvae were found in 21 fish species in the White Sea (Shulman and Shulman-Albova 1953), 7 species in the Barents Sea (Polyansky 1955), 25 species in far-eastern seas of the USSR (Strelkov 1960; Zhukov 1960; Mamaev et al. 1963; Skraybina 1963), 9 species in northern Japanese waters (Oshima 1972; Kagei 1974; Shiraki 1974), 7 species in the Bering Sea (Mamaev 1965), and 24 species in northwestern European waters, including the North and Baltic seas (Schuurmans Stekhoven 1935; Kahl 1938, 1939; Engelbrecht 1958; Berland 1961). A checklist of parasites of Canadian fishes, currently under preparation at the Pacific Biological Station, shows 26 species reported as hosts of codworm larvae on the Atlantic coast and 10 species on the Pacific coast. In southern hemisphere waters fewer surveys have been conducted on fish parasites and hence less information is available on the occurrence of codworm larvae. Johnston and Mawson (1945) list 11 or 12 fishes as hosts in Antarctic and subantarctic waters.

Although cod are generally regarded as the most frequent hosts of *P. decipiens* larvae, they are by no means always infected. Detailed quantitative analysis of codworm occurrence has been the subject of special studies in commercial-size cod from waters of northern Europe, Iceland, Greenland, and the Atlantic coast of Canada (Kahl 1939; Templeman et al. 1957; Scott and Martin 1957, 1959; Rae 1963, 1972; Wiles 1968; Young 1972; Platt 1975). These investigations demonstrated a marked geographic variability in the abundance of codworm larvae in cod muscle. Prevalences of infection varied from less than 1% in some offshore banks on the east coast of Canada and in the Barents and Baltic seas to as high as 70–90% in some areas such as the southern Gulf of St. Lawrence, the South Minch off the west coast of Scotland, and off the west coast of Iceland. Mean numbers of worms per cod ranged from 0.01 to 8 and mean numbers per kilogram of fillets varied from 0.02 to 5. In most areas investigated the prevalence of infection in cod fillets was less than 30% (many less than 10%), the mean number of worms per cod less than 0.4, and the mean number of worms per kilogram of fillets less than 0.5. Occasionally, entire samples of commercial-size cod from widely separated areas, such as the west coast of Greenland, offshore banks of eastern Canada, and waters around the British Isles, were completely free of *P. decipiens* larvae. Rarely, individual cod were encountered with large numbers (>100) of codworm larvae (Platt 1975). A notable feature of codworm infection is the increase in prevalence and mean numbers of worms per fish with increase in size (and age) of cod. Marked annual variations in these parameters have also been observed.

In contrast to the situation in cod, a report on the parasites of sockeye salmon (*Oncorhynchus nerka*) of the Pacific Ocean (Margolis 1963) may be cited to provide an example of a species of fish only lightly infected with codworm larvae throughout its distributional range. In a transpacific survey extending from British Columbia and Alaska to the Sea of Okhotsk, 30 (1.6%) of 1900 sockeye salmon were infected. Twenty-five fish harbored only 1 worm, the maximum number in a fish was 4 and the mean number per fish for all sockeye examined was 0.02.

Nomenclature of Human Disease Caused by Codworm

Various names have been applied to the human disease caused by codworm and its relatives. These include terranoviasis (or terranovasis), phocanemiasis, contracaeciasis, anisakiasis, anisakiniasis, anisakidiasis, and heterocheilidiasis. The pros and cons of these names have been discussed by Nagano (1974), Shiraki (1974), Suzuki et al. (1974), and Cheng (1976). The first two are specific, relating only to infections with codworm larvae, and depend on the choice of genera as a home for the codworm. The third is specific for infections caused by *Contracaecum*

and the last three are intended to be all-inclusive for human infections by larvae of members of the subfamily Anisakinae or family Anisakidae, which in earlier times were included in the family Heterocheilidae. Anisakiasis was originally proposed by van Thiel (1962) for larval *Anisakis* infections, but Cheng (1976) recommended a broader application to cover the disease syndrome caused by larval *Anisakis*, *Phocanema*, and *Contracaecum*. Jackson (1975) and Myers (1976) used anisakiasis in this broad sense.

For clinicians it may be satisfactory to adopt a broad use of anisakiasis to cover human infections with all larval anisakine or anisakid worms, but for those concerned with specific etiology this course of action is unsatisfactory. In this review I have refrained from using any of the above designations, although I was tempted to use phocanemiasis because the genus *Phocanema* will likely gain wide acceptance since its recognition in Anderson et al.'s *Keys to the Nematode Parasites of Vertebrates* (Hartwich 1974) and because it is likely monotypic. Phocanemiasis would thus denote infections only by *P. decipiens* larvae.

Another way out of the dilemma, which might satisfy both the clinician and the etiologist, is to restrict anisakiasis to its original use to denote infections with *Anisakis* larvae, to use "nonspecific anisakiasis" when the larva has not been identified to genus or as a collective term for infections with Anisakidae larvae, and "phocanemal (or terranoval) anisakiasis," "contracaecal anisakiasis," etc. for infections with larvae of the genera *Phocanema*, *Contracaecum*, etc. The question of whether to use phocanemal or terranoval anisakiasis will likely resolve itself shortly as *Phocanema* comes into standard use for the codworm.

Experimental Infections in Laboratory Animals

Concern about the role of *Anisakis* larvae in gastrointestinal disorders of man led to a rash of experimental studies of infections in guinea pigs, rats, rabbits, dogs, cats, monkeys and, most recently, pigs. These experimental investigations spilled over to include the codworm even before it was recognized that this worm can also produce an acute abdominal syndrome in man.

Otsuru et al. (1968) orally administered codworm larvae (taken from *Arctoscopus japonicus*) to rabbits and found they penetrated into the stomach wall and sometimes through to the body cavity within 3 h. Presumably reporting on the same experiments, Shiraki (1969) noted that of six rabbits force-fed 3–9 codworm larvae from four different fishes and autopsied 3–6 h post-infection, two rabbits had larvae (from *Arctoscopus japonicus*) penetrating into the stomach wall and one of them also had a larva that had penetrated through to the body cavity. On the basis of these results Otsuru et al. and Shiraki speculated that codworm larvae could penetrate into the wall of the stomach and intestine of man. Further evidence of the ability of codworm larvae to penetrate into the stomach wall of rabbits was obtained by Kikuchi et al. (1970, 1972) and Oishi et al. (1974). The larvae used in the experiments conducted by these authors were collected from Pacific cod (*Gadus macrocephalus*) and walleye (Alaska) pollock (*Theragra chalcogramma*).

In other experimental infections it has been shown that codworm larvae can partially penetrate into the stomach wall of rats (Young and Lowe 1969), dogs (Kikuchi et al. 1970, 1972), and pigs (Jackson et al. 1976). Young and Lowe and Kikuchi et al. obtained their worms from Atlantic cod (*Gadus morhua*) and Pacific cod, respectively; the source of those used by Jackson et al. was not stated.

According to Young and Lowe (1969) for rats and Jackson et al. (1976) and Bier et al. (1976) for pigs, penetration of the stomach wall and the host reaction was not as severe in larval *Phocanema* (*Terranova*) infections as in larval *Anisakis* infections. Penetration of the gastric mucosa by the former larva was superficial and involved only the head end of the worm, whereas the latter became entirely embedded in the gastric wall of pigs and in some cases in rats penetrated through the stomach wall to the body cavity. Oishi et al. (1974b), however, stated that *Terranova* (*Phocanema*) larvae showed greater "pathogenic capacity" than *Anisakis* larvae when introduced orally into rabbits, but they did not specify their criteria for assessing pathogenicity.

Natural Infections in Terrestrial Mammals

There is one report of *Phocanema* (as *Terranova*) larvae causing an eosinophilic granuloma of the stomach wall of a stray dog in Hokkaido, Japan (Kitayama et al. 1967). Pillers (1928), in England, reported a case of a dog vomiting *Porrocaecum decipiens* larvae after eating fresh haddock (*Melanogrammus aeglefinus*), but the larvae apparently were misidentified. Pillers' description of the larvae indicates that they belonged to the *Anisakis*-type (Johnston and Mawson 1945).

Human Cases of Codworm Infection

To date there have been reports of at least 46 individual cases of human infections with con-

TABLE 1. Summary of confirmed or presumed "codworm" infection in man, in chronological order of reporting.[a]

Type of infection[b]	Country	Sex and age of patient	Known or suspected source of infection	Reference
D	Greenland	♂ child	—	Martin (1921)
E	USA (Alaska)	—	—	Hitchcock (1950)
C	England	—	—	Buckley (1951)
B	USA (Mass.)	♂ 76	—	Little and MacPhail (1972)
A	Japan (Hokkaido)	♂ 17	raw Pacific halibut	Suzuki et al. (1972)
A	Japan (Hokkaido)	♂ 31	raw undetermined sea fish	Suzuki et al. (1972)
A	Japan (Hokkaido)	♀ 45	raw undetermined sea fish	Suzuki et al. (1972)
A	Japan (Hokkaido)	♂ 27	raw Pacific halibut[c]	Suzuki et al. (1972)
A	Japan (Hokkaido)	♂ 26	raw Pacific cod	Suzuki et al. (1972)
A	Japan (Hokkaido)	♀ 31	marinated *Pleurogrammus azonus*	Kagei et al. (1972) Nagano et al. (1973)
C	USA (New York)	♀ 24	marinated ("ceviche") sea fish	Little and Most (1973)
C	Canada (N.S.)	♀ 22	lightly cooked Atlantic cod	Kates et al. (1973)
A	Japan (Hokkaido)	♂ 39	raw Pacific halibut	Doi (1973)
A	Japan (Hokkaido)	♂ 38	raw Pacific halibut	Doi (1973)
A	Japan (Hokkaido)	♀ 35	raw Pacific halibut	Doi (1973)
A	Japan (Hokkaido)	♀ 39	raw Pacific halibut[c]	Doi (1973)
A	Japan (Hokkaido)	♂ 27	raw Pacific cod	Doi (1973)
A	Japan (Hokkaido)	♀ 43	raw Pacific cod	Doi (1973)
A	Japan (Hokkaido)	♀ 44	raw Pacific halibut[c]	Doi (1973)
A	Japan (Hokkaido)	♂ 23	raw Pacific halibut	Doi (1973)
A	Japan (Hokkaido)	♀ 24	raw squid	Doi (1973)
A	Japan (Hokkaido)	♂ 36	raw "flounder"	Doi (1973)
A	Japan (Hokkaido)	♂ 57	lightly marinated Pacific cod	Nagano et al. (1974)
A	Japan (Hokkaido)	♀ 53	raw Pacific cod	Nagano et al. (1974)
A	Japan (Hokkaido)	♀ 48	lightly cooked *Sardinops* sp.	Nagano et al. (1974)
A	Japan (Hokkaido)	♀ 55	raw *Sebastes* sp.	Nagano et al. (1974)
A	Japan (Hokkaido)	♂ 35	raw Pacific cod	Nagano (1974)
A	Japan (Hokkaido)	♂ 62	raw Pacific cod	Nagano (1974)
A	Japan (Hokkaido)	♀ 34	marinated Pacific cod	Nagano (1974)
C	USA (Calif.)	♂ 13	marinated ("ceviche") red snapper	Chitwood (1975)
C	USA (Calif.)	♂ 44	raw "white sea bass"	Juels et al. (1975)
A[d]	Japan (Hokkaido)	—	—	Koyama et al. (1976)
C	USA (Alaska)	♂ 46	—	Lichtenfels and Brancato (1976)

[a]A case reported by Chitwood (1970), although involving a nematode larva of the *Phocanema–Terranova–Porrocaecum* type, is not included because on morphological grounds the larva apparently does not belong to *Phocanema decipiens*. In length of intestinal cecum (longer than ventriculus) and absence of a tail mucron, it resembles *Terranova* sp. larva Type B of Koyama et al. (1969), described from Japanese fish.

[b]A, Acute abdominal syndrome due to penetration of stomach mucosa by anterior end of worm. B, Asymptomatic; worm recovered accidentally during abdominal surgery for other purposes. C, Asymptomatic; worm coughed up or manually removed after migration from stomach to throat or mouth. D, Worm expelled by vomition. E, Asymptomatic; worm expelled in feces.

[c]Patient also consumed one or more of raw tuna, squid, or yellowtail (*Seriola quinqueradiata*) at same meal.

[d]Represents 19 cases for which information on the patients and probable source of infection is not available in Koyma et al. (1976). These cases probably include the 5 reported by Suzuki et al. (1972) because they are from the same hospital and the year of occurrence falls within the years covered by the 19 cases.

firmed or presumed larval codworms (Table 1). They can be divided into four categories: 37 clinical cases due to penetration of the stomach mucosa by the anterior end of the worm; 1 case in which the worm was found incidentally in the vicinity of an aneurysm of the right common iliac artery after surgery for removal of the artery; 1 case in which the worm was expelled by vomition; 6 cases in which the worm temporarily occurred in the stomach from where it migrated to the throat and was coughed up or manually removed; and 1 case in which the worm was expelled in the feces. Interestingly, there are no known cases of intestinal wall invasion such as commonly found in *Anisakis* infections.

In addition to the 46 cases listed in Table 1,

there are an undetermined number of cases from Japan in which nematode larvae, some of which might have been codworm, were expelled by vomiting or were coughed up after eating raw fish (Nagano 1974). Acute abdominal symptoms that occurred in some of these cases disappeared after the worm was voided.

Several features of the 46 cases summarized in Table 1 are particularly noteworthy. Analyzed by country, there were 37 from Japan (all from Hokkaido), six from the USA, and one each from Canada, England, and Greenland. The North American cases were confined to Atlantic and Pacific coastal regions where fresh raw fish are most likely to be available. All cases from Japan were of the clinical variety involving penetration into the stomach mucosa. Cases from the other countries were nonclinical and eight of the nine were detected only when the worm was expelled orally or in the feces. A single case in the USA was detected accidentally in pathological material removed during abdominal surgery for an unrelated ailment.

There was no sex preference either in clinical or nonclinical infections and cases were found among all age groups from teenagers to septuagenarians.

Cod and Pacific halibut (*Hippoglossus stenolepis*) were the main sources of the reported cases of codworm infection in man, at least in Japan, but other fishes were also involved (Table 1). Squid, probably *Todarodes pacificus*, have also been implicated.

The principal symptom in clinical cases is severe epigastric pain, sometimes accompanied by nausea and vomiting or other abdominal discomfort. For 22 cases it is known that pain, sometimes spasmodic and occurring every 3–10 min, commenced 2–10 h after eating raw fish (Suzuki et al. 1972; Doi 1973; Nagano et al. 1974; Nagano 1974) and persisted until the patients presented themselves for medical examination 6 h to 10 days after the onset of abdominal symptoms. Within a few hours to several days after removal of the worm with a gastrofiberscopic biopsy forceps, the pain disappeared and the patient returned to normal health.

Pathological changes evident when the stomach wall is viewed by gastroscopy may include edema, inflammation, thickening of the mucosa, and bleeding at the point of codworm penetration, although in some instances there is almost no visible local alteration in the tissues (Doi 1973; Nagano 1974).

In three North American cases of oral expulsion of the worm for which appropriate information is available, 4–10 days elapsed from ingestion of apparently infected fish to voiding of the live worm. Because of the absence of abdominal symptoms in North American cases involving oral expulsion of a live worm, it is assumed that the worm remained in the stomach lumen without invading gastric tissues. Juels et al. (1975) referred to these as lumenal infections. However, they noted that the possibility of asymptomatic temporary invasion of the gastric wall could not be ruled out in the case they investigated because the patient exhibited a slight eosinophilia.

One can only speculate on the reasons for the absence in North America and Europe of clinical cases with acute symptoms. The possibility that *P. decipiens* larvae in fishes landed in Japan have a greater tissue penetrating ability than those occurring in fishes in North America and Europe can be ruled out. Pacific halibut, the reported source of some Japanese clinical cases, are caught in the same northern Pacific waters as halibut landed and marketed in North America and hence are infected with the same populations of *P. decipiens* larvae. Other fishes along the Pacific coast of North America carry *P. decipiens* larvae belonging to populations that probably are not genetically distinct from those occurring in halibut because the North Pacific fur seal (*Callorhinus ursinus*), a common definitive host of *P. decipiens* (see Margolis and Dailey 1972), annually migrates between breeding areas in the Bering Sea and the waters off the California coast. These and other migrations of the pinniped definitive hosts and of some of the fish hosts would prevent isolation in the North Pacific of populations with genetically controlled differences in tissue-penetrating ability of the larvae. The experimental work of Young and Lowe (1969) and Jackson et al. (1976) has shown that codworm larvae from the eastern and western North Atlantic can penetrate the gastric mucosa of rats and pigs. Finally, the finding of a codworm larva in the body cavity of a man in Massachusetts (Little and McPhail 1972) provides evidence of the tissue-penetrating ability of Atlantic populations of this worm. Hence, it is not likely that there are differences in penetration ability between Pacific and Atlantic populations of codworm.

A possibility to be considered is that physicochemical conditions in the stomach affect penetration by codworm larvae and that these conditions differ between Japanese and occidentals because of dietary differences. With the related *Anisakis* larva, for example, gastric mucosal penetration in guinea pigs appears to be favored by hypoacidity (Asami and Inoshita 1967).

Possibly the absence of any records of clinical

cases in western nations may be due to unfamiliarity among physicians in most of these countries with the acute abdominal syndrome associated with human infections by fish-carried anisakine worms (*Anisakis*, *Phocanema*). In Japan, where this disease complex has been most intensively studied, more than 1000 cases of *Anisakis* infection have been reported from man (Myers 1976), and the public as well as the medical profession have been apprised of this disease syndrome and its causes.

Diagnosis, Treatment, and Prognosis

Because the symptoms of codworm infection in man are not specific, clinical features alone are insufficient for positive diagnosis. Presence of a worm penetrating the gastric mucosa may be detected by X ray (Kagei et al. 1972), and Doi (1973) indicated that X ray and endoscopy may be useful tools in diagnosis, even to the extent of enabling one to distinguish between *Anisakis* and *Phocanema* larvae. Positive diagnosis, however, can only be made by recovery and identification, on morphological grounds, of the codworm larva. In suspected cases of gastric wall invasion, location and removal of the worm can be achieved with the aid of a gastrofiberscope fitted with forceps (Oshima 1972; Suzuki et al. 1972; Nagano et al. 1974). Intestinal wall infections, none of which have yet been found, could only be positively diagnosed after resection of the worm-containing tissue, as in the case with intestinal infections by *Anisakis* larvae (Oshima 1972).

Techniques for immunodiagnosis of human codworm infection have not been specifically investigated. However, attempts to develop intradermal or serodiagnostic tests for detection of larval *Anisakis* infections have not yet yielded a practical and totally reliable method for routine application (Oshima 1972). Immunofluorescent and radioimmunoassay tests seem to offer the best promise (Ruitenberg 1970; Suzuki et al. 1974, 1976).

If stomach wall infections are correctly diagnosed and the worm removed with a gastrofiberscopic biopsy forceps, recovery is rapid. If untreated, pain can persist for 10 days and possibly longer. Presumably, the pain would ultimately subside when the worm either dies and degenerates within the stomach or is expelled orally or in the feces. Cases of spontaneous cure have been noted by Nagano (1974), and Doi (1973) stated that in untreated cases symptoms disappear within "a comparatively short period of time" and there are no aftereffects. In experiments with pigs (Jackson et al. 1976) and rats (Young and Lowe 1969), *P. decipiens* larvae completely disappeared between 10 and 14 days in the former animal and after 7 days in the latter. A similar short life within the human body might also be expected.

Because all North American cases reported to date have been asymptomatic and, with one exception, have been recognized only when the worm was expelled from the body, no medical importance can be attached to these cases. At most, the patients may have experienced temporary mild shock.

Prevention

The source of human codworm infection is raw, lightly marinated, or undercooked marine fishes belonging to a variety of species. Prevention of infection can only be assured by processing fish prior to eating in such manner that ensures death of codworm larvae. Attempts to remove the larval worms from cod fillets in fish processing plants in eastern Canada by "candling" have not been entirely successful (Power 1958, 1961). Some worms, especially those deeper in the fillet, inevitably escape detection.

Based on studies by Ronald (1960) on *P. decipiens* larvae and by others on *Anisakis* larvae, Bier (1976) concluded that to kill anisakine larvae fish should be cooked so that the internal temperature reaches a minimum of 60°C for 1 min. However, it is questionable if the data on *P. decipiens* larvae can be interpreted in this way. Ronald reported time to mortality of codworm larvae exposed to various temperatures within 30-mm (approximately 1.2 in.) cubes of fish muscle and in a saline medium. In the fish muscle worms were killed in 7 min at 70°C, 10 min at 60°C, approximately 50 min at 50°C, and almost 2 h at 45°C. Time for the internal temperature of the fish cubes to reach these temperatures apparently was not measured. In a saline medium the larvae are killed instantly at 70°C, within 1.5 min at 60°C, within 13 min at 50°C, and within 32 min at 45°C. Translated into practical conditions, starting from room temperature it appears that cooking of 30-mm thick fish fillets at 70°C for 7 min or at 60°C for 10 min should kill any codworm larvae that may be present. Therefore, normal cooking procedures would be lethal to codworm larvae. In the face of Ronald's results, Vitzhum's (1933) report of survival of larave in marinated cod boiled for 20 min must be discounted.

Low temperatures are also effective in killing codworm larvae. Ronald (1960) determined that at −20°C larvae in cod flesh are killed in less than 24 h. At lower temperatures the time to

death is reduced: at −30°C, less than 5 h; at −40°C, 40 min; and at −50 to −70°C only a matter of minutes. Taking into consideration data on *Contracaecum* larvae (Bier 1976), it has been recommended that in commercial and home freezing fish be held at −20°C for 60 h (Myers 1976) to kill anisakine larvae.

An early report (Williamson 1911) indicates that codworm larvae can survive smoking of lightly marinated cod fillets for ¾ to 2 h, but the temperature during the smoking process was not given.

Oishi et al. (1974a) investigated the effects of some spice essential oils and their principal components on survival of codworm larvae collected from Pacific cod and walleye pollock. Survival in extracts of cumin, clove, allspice, cinnamon, thyme, dill, and caraway and in cumin aldehyde, cinnamic aldehyde, thymol, limonene, and euganol was markedly less than control worms. The relationship of these findings to practical application in marinating or other methods of processing and preserving fish products was not discussed.

Various studies have been conducted on the effects of brine curing, smoking, irradiation, and a number of marinating procedures on survival of *Anisakis* larvae in fish products, but similar studies have not been done with codworm larvae.

Thus, in the present state of knowledge, the only effective treatment for killing codworm larvae in fish muscle is freezing or cooking as described above.

Public Health Implications

In Japan, where acute clinical infections have been reported and where raw sea fish is consumed in large quantities, codworm is of some public health concern. Elsewhere, however, in the absence of clinical infections, it is doubtful whether codworm can be given the same status.

The relative ease with which codworm larvae can be killed through freezing or cooking and the food habits of most North Americans are sufficient to keep the codworm from becoming a public health problem on this continent, although occasional cases may occur. Indeed, the same can be said for most countries of the world.

While it may be true, as Jackson (1975) has written, that eating raw or undercooked fish is increasing in North America, nevertheless the proportion of the population indulging in such culinary dishes and the per capita consumption of them must be insignificant.

Even in Japan, where raw sea fish constitutes a regular part of the diet in a population numbering more than 110 million and awareness among the medical profession of the anisakid syndrome in man is high, there are less than 40 known confirmed cases of human codworm infection, dating from 1969. This implies that many live codworm larvae that are ingested must either pass through the gut (dead or alive) or are digested without producing any clinical symptoms. Similar views have been expressed with respect to ingested *Anisakis* larvae (Ruitenberg 1971; Oshima 1972, 1974).

By contrast with *Anisakis* infections in man, codworm infections are much less common and apparently less severe. Whereas fewer than 50 human cases of codworm infection have been documented, more than 1200 cases of *Anisakis* infection have been reported in the last 15 yr. Tissue penetration is usually more superficial in codworm infections, which in man have been almost entirely confined to the stomach. Intestinal invasion, unknown in human codworm infections, is common among *Anisakis* infections. Hence, removal of the worms (resulting in alleviation of symptoms) with the aid of a gastrofiberscope has been possible in all clinical codworm cases but not in all *Anisakis* cases. More drastic surgical procedures for removal of the worm have been required in intestinal *Anisakis* infections (Oshima 1972).

Apparently the tendency or ability of codworms to penetrate tissue is less than that of *Anisakis* larvae, which may explain the relative scarcity of clinical codworm infections in man.

Accidental ingestion of dead codworm larvae in cooked or previously frozen fish is not likely to have any harmful effects on health. Crampton et al. (1960), experimenting with pups, found no adverse effects on growth, feed consumption, efficiency of feed utilization, and general health of animals fed codworm larvae that had been frozen previously and were therefore presumably dead.

In summary, while individual human cases of codworm infection probably will continue to be found, particularly where raw sea fish constitutes a dietary staple, codworm will not likely become a serious public health problem on a global basis.

Some Future Research Needs

Much remains to be learned or verified of the basic biology of *P. decipiens*. Some aspects of the life cycle are still equivocal, e.g. the identity of the first intermediate host, the role of fish as true intermediate or paratenic hosts, and the number of molts within the definitive hosts. Even something as fundamental as the generic allocation of this species remains unsettled.

However, in relation to the public health question, there are a number of specific avenues of research that should be followed. These can be grouped under Prevention, Diagnosis, Treatment, and Epidemiology.

Prevention

High and low temperatures lethal to codworm larvae should be reexamined to confirm and extend Ronald's (1960) observations. Experiments should be conducted that duplicate methods of commercial and home freezing of fish and various ways of cooking. Effects on codworm survival of salting, drying, smoking, and other methods of processing fish also need investigation. It is important to determine effects of various treatments not only on survival but on infectivity of the larvae. Viable larvae are not necessarily infective.

Improvement in methods of detection and removal of codworm from fillets and development of techniques of treating fillets to induce the worms to leave voluntarily should be pursued vigorously in an attempt to market worm-free fillets. This is probably more important from the aesthetic than the public health point of view.

Diagnosis

Development of a specific and reliable immunodiagnostic technique would be an asset, particularly in detecting asymptomatic cases in surveys designed to assess the prevalence of human codworm infection. Use of an immunodiagnostic technique to confirm clinical diagnoses of acute gastric infections would also be valuable, but may not be realistic because of the early onset of symptoms (within hours of ingesting a live worm), during which time detectable antibodies may not yet be present.

Improved criteria for distinguishing codworm from other nematode larvae in histopathological sections is required.

Treatment

At present the only treatment for gastric mucosal infections with codworm is removal of the worm with the aid of a gastrofiberscope. This can sometimes be a traumatic experience for the patient (Nagano 1974). Therefore, it would be useful if an anthelmintic treatment were available. Such treatment would be especially valuable in the event intestinal cases are discovered (and detectable by immunodiagnostic methods), because otherwise they could only be treated by laparotomy and resection of the affected region of the intestine as is now done in intestinal *Anisakis* infections.

Epidemiology

There remains the perplexing question of why only an apparently small proportion of larval codworms invade gastric tissues and produce clinical symptoms in man. To better understand this phenomenon, further studies are required to identify host and parasite factors affecting infectivity in nondefinitive mammalian hosts.

Acknowledgments

I thank Dr. T. Oshima, Yokohama City University, for providing and translating some Japanese literature and Mr T. Isogai, Director, International North Pacific Fisheries Commission, and Mrs M. Miki, Nanaimo, for kindly translating several papers. Dr R. J. Lichtenfels kindly made available a prepublication copy of his paper cited in this review.

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Heavy-Metal Contamination by Atmospheric Fallout of Several Flin Flon Area Lakes and the Relation to Fish Populations

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VAN LOON, J. C., AND R. J. BEAMISH. 1977. Heavy-metal contamination by atmospheric fallout of several Flin Flon area lakes and the relation to fish populations. J. Fish. Res. Board Can. 34: 899–906.

High concentrations of zinc and other heavy metals were found in lakes in the immediate vicinity of the Flin Flon smelters. In a study of 31 lakes, 7 had Zn levels above 100 $\mu g/\ell$, 6 had levels between 50 and 100 $\mu g/\ell$, and the remainder had concentrations <50 $\mu g/\ell$. The accuracy and precision of the heavy metal chemical analyses were evaluated using intercomparisons with other laboratories and a standard reference water. A linear relationship was demonstrated between $\log_{10}$ concentration of Zn, Cu, and SO_4^{2-} and $\log_{10}$ distance from the smelter, suggesting atmospheric fallout as the main source of these substances in the lakes. Fishes were more tolerant of these high zinc concentrations than would be expected on the basis of the responses of fish and other aquatic organisms to similar concentrations of zinc in some laboratory toxicity tests.

Key words: heavy metals, zinc, atmospheric fallout, fish toxicity, lake contamination, chemical analysis, Flin Flon, Canada

VAN LOON, J. C., AND R. J. BEAMISH. 1977. Heavy-metal contamination by atmospheric fallout of several Flin Flon area lakes and the relation to fish populations. J. Fish. Res. Board Can. 34: 899–906.

Nous avons trouvé de hautes concentrations de zinc et autres métaux lourds dans les lacs situés dans le voisinage immédiat des hauts fourneaux de Flin Flon. Sur 31 lacs étudiés, 7 ont des niveaux de Zn dépassant 100 $\mu g/\ell$ 6 entre 50 et 100 $\mu g/\ell$, et la balance ont des teneurs <50 $\mu g/\ell$. Des comparaisons avec d'autres laboratoires et avec une eau-étalon nous ont permis de vérifier la précision des analyses chimiques de métaux lourds. Nous démontrons une relation linéaire entre le $\log_{10}$ de la teneur en Zn, Cu et SO_4^{2-} et le $\log_{10}$ de la distance du haut fourneau, ce qui donne à croire que la retombée atmosphérique est la principale source de ces substances dans les lacs. Les poissons tolèrent mieux ces hautes teneurs en zinc qu'on s'y attendrait en se basant sur leur réponse et celle d'autres organismes aquatiques à de semblables concentrations de zinc dans certains essais de toxicité en laboratoire.

Received January 13, 1975
Accepted February 16, 1977

Reçu le 13 janvier 1975
Accepté le 16 février 1977

THERE are at least two major problems associated with the setting of "safe" limits for metals in the aquatic ecosystem. Firstly, interlaboratory comparison studies on metal analysis, e.g. Uthe et al. (1971), Van Loon (1974), and Lauwerys et al. (1975), have indicated that variability obtained is often so high as to cast doubt on the validity of much of the metal data now in the literature. Secondly, there is very little information concerning the response of fish populations to gradual accumulations of sublethal or chronic concentrations of heavy metals in natural aquatic systems.

The purpose of this work was to examine the response of fishes in natural lake systems to sublethal concentrations of Zn or mixtures of Zn and other metals. A study of the condition of fish populations was undertaken from a selection of lakes with varying Zn and other heavy-metal levels. The area near Flin Flon, Manitoba, was selected because the possibility existed that the lakes, of almost neutral pH in this vicinity, had been contaminated by atmospheric fallout containing heavy metals.

Printed in Canada (J4161)
Imprimé au Canada (J4161)

Materials and Methods

Study Area

Flin Flon, Manitoba, is located on the Manitoba–Saskatchewan border at roughly 55°N, 102°W (Fig. 1). A Cu, Zn, Ag, Au sulfide ore has been mined and smelted at this location since 1930. Production is presently 4172 t/day. Winds in the area (Fig. 2) which intersect the stack gases, blow in a predominantly northwest, southeast direction (Monthly record of meteorological observations in Canada). Atmospheric fallout from stack emissions contains sulfur acids and metal-bearing aerosols. Until recently, stack heights were < 30 m. Now, in an effort to dilute contamination close to the smelter, a tall stack is in operation. Tailings are dumped into Flin Flon Lake (Fig. 1) which is now nearly obliterated. Water drainage occurs from Flin Flon Lake through Ross Lake into the northwest arm of Schist Lake. Cliff Lake, northeast of Flin Flon, is the town water supply.

Sampling and Sample Preservation

A clean Van Dorn water sampler was used to collect 1-ℓ water samples at 1 m depth from 31 lakes. One sample was taken near the center of each lake. In Hamell, Cliff, and Ross lakes, samples were taken at up to five locations and at approximately 2-m depth intervals to the bottom. Spring, summer, and fall sampling programs were carried out over the period 1973–74.

All samples for pH were placed in nonacid-washed, high-density, linear polyethylene bottles. Determinations of pH were made at 20°C within 2 h of completion of sampling. A Radiometer Model 53 Specific Ion Meter, calibrated prior to each set of determinations using pH 4 and 7 buffers, was used. Water for heavy metal analysis was stored in acid-washed, high-density, linear polyethylene bottles at 4°C.

"Dissolved" metal concentrations were obtained by filtering a sample immediately after collection through an acid-washed and distilled-water-rinsed 0.45-μm porosity membrane filter. The filtrate was acidified with 3 ml of 1:1 HNO_3 for every 1000 ml of sample as recommended by the EPA (1971).

"Total" metal was determined from an unfiltered sample that was collected and acidified at the site. In the laboratory a suitable volume of the sample was placed in an acid-washed beaker and evaporated to near dryness in the presence of HNO_3. A blank was run with each sample set.

Sulfate, calcium, magnesium, and pH were determined from nonacidified samples according to the procedures of Stainton et al. (1974). Alakalinity was not determined.

Heavy Metal Analyses

A solvent extraction–atomic absorption procedure similar to that of Kinrade and Van Loon (1974) was used. A solution of two chelating agents, 1% ammonium pyrolidine dithiocarbamate (APDC) and 1% diethyl ammonium diethyl dithiocarbamate (DDDC) in water, was employed to extract heavy metals into methylisobutyl ketone (MIBK). An acetate buffer

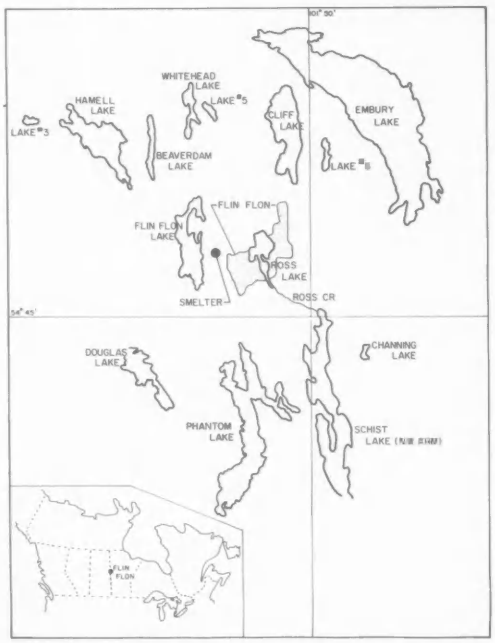

FIG. 1. Flin Flon, Manitoba, area.

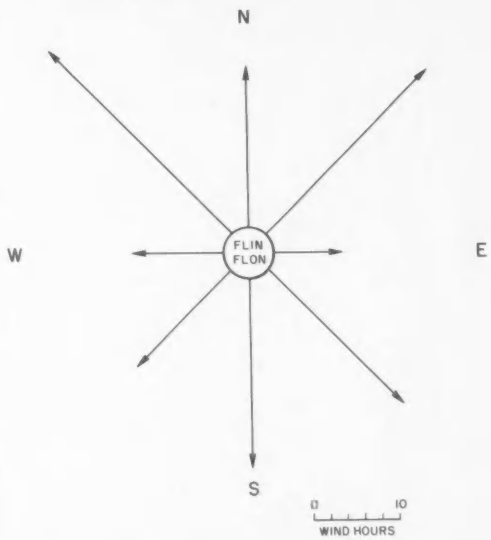

FIG. 2. Summary of winds in the Flin Flon area.

was used. Stock solutions were prepared by dissolving pure metals in acid. Heavy-metal working solutions were prepared fresh each day.

Appropriate volumes of working solutions, samples, blanks and EPA-1 were placed in separatory funnels equipped with Teflon stopcocks. The extraction was done at pH 4. A control sample (EPA-1) was run with every 20 samples. Blanks were included with each sample set. An Instrumentation Laboratories Model 153 equipped with a three-slot burner was used. The spectral lines employed were 324.7 nm Cu, 213.9 nm Zn, 248.3 nm Fe, and 228.8 nm Cd.

Brungs et al. (1976) point out that, currently, toxicity studies should be based on dissolved quantities of metal determined after 0.45-μm filtration. To examine the chemical form of the Zn in Hamell Lake, an unacidified sample was taken in the spring of 1974. Samples of water were analysed before and after filtration through 60-, 5.0-, 0.45-, and 0.2 μm porosity filters. All the samples were acidified after filtration and evaporated in the presence of strong acid. Hamell Lake water, filtered through 0.45-μm filters, was also analyzed by DC differential pulse polarography using a P.A.R. Model 174 polarograph.

Fish Study Method

Eight of the lakes with the highest Zn concentrations, ranging from 50 to 8000 $\mu g/\ell$, were fished with gill nets of stretched-mesh size ranging from 18 to 100 mm. Ross, Hamell, and Cliff lakes were fished with approximately 600 m of gillnet. Embury, Phantom, Whitehead, Douglas, and Lake No. 6 were netted with 50–125 m of the variable-mesh nets. Fish were measured for fork length and weighed, and the condition of the ovaries was noted. Scales were taken from selected samples of fish for age determination.

Chemical Analysis

Because of the lack of acceptable standard reference samples, it is difficult to assess the precision and accuracy of analytical methods for the determination of metals in water. The U.S. Environmental Protection Agency has issued three water–trace standards, designated EPA-1, EPA-2, and EPA-3. EPA-1, one sample with every 20 unknowns, was used as a control throughout this study and was analyzed 10 times.

Recognizing the need to have a further assessment of accuracy, we undertook an interlaboratory comparison of heavy metal analyses with three other laboratories.

In the analysis of water, where micrograms-per-litre levels are being measured, blanks are crucially important. All data reported were corrected for blanks. Samples of lake water, obtained as described above, were analyzed for SO_4^{-2}, Fe, Cu, Cd, Zn, Ca, and Mg. The pH was also determined.

Results and Discussion

Standard deviations obtained from a metal analysis of the EPA-1 water standard show that adequate precision was obtained (Table 1). Acceptable agreement with analyses of other laboratories was obtained for all heavy-metal elements and in all samples except for Cu and Pb in Swedish lake samples (Table 1). The good agreement obtained for these two elements in other sample types, including the EPA-1 standard reference sample, suggests that the results in this study are accurate. Spiking and other "accuracy" tests, involving the addition of metal standard solution to the sample, were not done because of the well-known pitfalls of these approaches.

Of the 31 lakes surveyed, 7 had average Zn concentrations > 100 $\mu g/\ell$, 3 lakes had concentrations ranging from 51 to 100 $\mu g/\ell$, 8 had concentrations ranging from 11 to 50 $\mu g/\ell$, and 12 had concentrations of $\leqslant 10$ $\mu g/\ell$ (Table 2). Ross Lake had excessive concentrations of almost all chemicals measured. The northwest arm of Schist Lake also contained high concentrations of Cu, Cd, and Zn, similar to concentrations found by other workers (Crowe 1973). Lakes farthest from the smelter had the lowest

Table 1. Interlaboratory study of the metal content of freshwaters. Average values are presented, with standard deviations in parentheses.

	Our lab ($\mu g/\ell$)	Other lab(s) ($\mu g/\ell$)
Swedish lakes		
Zn	36	44
	42	48
Cu	2	0.4
	2	0.4
Ni	3	3
	2	2
Pb	4	<0.1
	7	0.1
Fe	93	124
	43	38
Cd	0.3	<0.5
	0.3	<0.5
Tap water		
Pb	4	4
	9	6
	300	330
River water		
Fe	260	300
Zn	18	18
Cu	35	33
Pb	2	1
EPA-1[a]		
Zn	8 (2)	10
Cd	2 (0.5)	1.8
Fe	25 (3)	18
Pb	33 (4)	28
Cu	8 (1)	9

[a]Accepted values.

TABLE 2. Chemical variables (0.45 μm filtered). Values represent four sampling periods. —, indicates no value available; *, receives effluent.

Lake	Distance from smelter (km)	pH	Ca (mg/ℓ)	Mg (mg/ℓ)	SO_4^{2-} (mg/ℓ)	Fe (μg/ℓ)	Cu (μg/ℓ)	Cd (μg/ℓ)	Zn (μg/ℓ)
Ross*	1.8	4.0	210	20	550	1600	450	50	8000
Beaverdam	3.5	7.5	40	6	30	54	23	1	450
Lake 6	5.0	7.9	15	4	15	30	12	0.5	150
Lake 5	5.0	7.7	7	2	10	68	13	0.5	110
Douglas	5.0	8.1	24	4	20	10	8	0.3	60
Cliff	5.3	7.6	16	4	16	10	10	0.4	85
Whitehead	5.3	8.0	16	2	8	100	10	0.5	150
Hamell	5.8	7.8	16	3	13	15	11	0.6	300
Channing	6.3	8.1	35	5	23	10	2	<0.2	25
Phantom	7.3	8.8	18	5	19	20	5	0.3	55
Schist N.W.*	7.5	6.2	30	4	30	20	13	5	1300
Schist Main	—	7.5	15	2	15	8	5	0.2	170
Lake 4	8.0	7.5	10	2	17	50	10	0.6	50
Lake 3	8.0	7.5	12	3	10	100	8	0.4	50
Embury	8.2	7.7	14	4	16	15	10	0.4	50
We	11.0	7.6	13	5	12	50	6	<0.2	15
Wonderland	11.0	7.5	13	5	13	50	6	<0.2	18
Johnson	12.0	7.8	8	2	10	30	3	0.2	10
Little Spruce	12.0	8.3	30	11	33	50	3	<0.2	5
Nesootao	12.5	7.6	—	—	12	26	8	0.2	30
Mosher	15.0	—	—	—	15	43	4	<0.2	17
Scottie	15.0	8.3	6	2	—	5	1	<0.2	2
Bluenose	17.0	8.2	6	3	6	9	2	<0.2	5
Kisseynew	20.0	—	—	—	5	90	1	<0.2	1
Neso	24.0	7.7	8	3	6	40	2	<0.2	1
Twin	30.0	7.9	12	3	6	62	1	<0.2	5
Naosap	30.0	7.6	—	—	6	50	2	<0.2	7
Maskunow	33.0	7.5	6	2	8	200	<1	<0.2	1
Otter	33.5	7.7	10	4	8	150	2	<0.2	4
Maligne	50.0	8.2	14	4	5	22	2	<0.2	1
Winteringham	70.0	7.8	6	2	5	30	<1	<0.2	1

concentrations of heavy metals which were similar to mean concentrations found in 109 relatively unpolluted lakes in northwestern Ontario (Beamish et al. 1976). Other metals, such as Ni, Hg, As, and Pb, were analyzed but values were very low or showed no trend. Of these, in a grossly contaminated lake such as Ross Lake, As, Hg, Ni, and Pb were 5, 6, 30, and 80 μg/ℓ, respectively. This compares with 0.5, 0.8, < 1, and < 1, respectively, for an uncontaminated lake (Van Loon unpublished data).

Fish were surviving in Hamell Lake despite the high concentrations of Zn. To see whether Zn was dissolved or particulate in form, filtration studies were done showing the following results:

Filter size (μm)	Zn (μg/ℓ)
No filtration	Variable ~ 1000
60	350
5	340
0.45	380
0.2	350

Toxicity to fish is dependent on the form of the metal (Brungs et al. 1976). From the text table it can be seen that any metal which passes the 60-μm filter also passes the 0.2-μm filter. Hence, the 350 μg/ℓ Zn in the spring sample of 1974 Hamell Lake water is either very finely divided or soluble. By EPA definition (1971), it is soluble.

Polarographic analysis of Hamell Lake water was accomplished to determine whether the Zn was bound or free. The amount of Zn found is as follows:

Sample treatment	Zn (μg/ℓ)
Acidified	240
Nonacidified	260
Acidified–evaporated	340

Analysis of the acidified–evaporated sample of Hamell Lake water gave 340 μg/ℓ Zn. This agrees well with 350 μg/ℓ Zn obtained for this sample by atomic absorption. A nonacidified sample

analyzed by polarography gave 260 $\mu g/\ell$ Zn. The one-half wave potential for the Zn reduction in all cases, above, was the same and corresponded to the value obtained from a reduction of Zn in a simple Zn–HNO_3 standard solution. These data suggest that up to 260 $\mu g/\ell$ Zn is not very strongly complexed by either organic or inorganic species.

Atmospheric Fallout

Ross and Schist lakes receive effluent from the smelter operation. Hence, these lakes were excluded from the calculations to determine the relationship of atmospheric fallout to lake chemistry. There was a strong linear relationship found between $\log_{10}$ Zn, Cu, and SO_4^{-2} and $\log_{10}$ distance from the smelter as follows:

For Zn, $\log y = 3.51 - 2.13 \log x$
$r = -0.90$, $F = 18.9$, significant at $P > 0.05$
For Cu, $\log y = 1.70 - 1.01 \log x$
$r = -0.84$, $F = 19.6$, significant at $P > 0.05$
For SO_4^{-2} $\log y = 1.59 - 0.505 \log x$
$r = -0.74$, $F = 88.0$, significant at $P > 0.05$

No linear relationship was found between Fe, pH, and distance from the smelter.

Fish Study

Hamell Lake — Hamell Lake is a moderately small shallow lake with a surface area of approximately 250 ha and estimated maximum depth of 5 m. Most of the lake ranges from 1 to 2 m deep. Dissolved Zn concentrations in July, September, and October 1973 were similar, ranging from 130 to 160 $\mu g/\ell$. Concentrations in a vertical profile varied by only 5 $\mu g/\ell$ in one series of determinations, and concentrations from five stations around the lake varied between 130 and 150 $\mu g/\ell$. In May 1974 three stations around the lake ranged from 260 to 350 $\mu g/\ell$ of Zn. Samplings at other times gave values up to 360 $\mu g/\ell$ Zn. The value of 300 $\mu g/\ell$ given in Table 2 is an average of all determinations. Average values for Cu in 1973 and 1974 were 9 and 15 $\mu g/\ell$, respectively.

Despite these rather high heavy-metal concentrations, the lake supported populations of walleye (*Stizostedion vitreum vitreum*), yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), white sucker (*Catostomus commersoni*), and possibly other species. Among the captured fishes, 8 walleye ranged in age from 4 to 10 yr, northern pike and white suckers included at least the last six year-classes (1973–68), yellow perch varied from young of the year to mature older fish, and 28 lake whitefish were age 3–10 yr. None of the fish, except perhaps the yellow perch, was stunted. The sample size of most species was not large enough to determine if some younger year-classes were absent. However, the presence of young-of-the-year yellow perch, northern pike, and white suckers indicated that at least some of the species had reproduced in the Zn concentrations measured during the study. The capture of young fish is always a problem and the failure to catch young-of-the-year walleye and lake whitefish does not indicate that they were absent. An examination of the ovaries of females did not suggest any abnormal development was occurring. There was little doubt that these species had been able to reproduce, grow, and survive in this lake.

It was not possible to estimate the population size for the various species in Hamell Lake. If the number of species captured per unit length of gillnet set was compared with catches from other nearby lakes (Table 3), then Hamell Lake appears to have smaller densities of some species. However, the size of a gillnet catch can be related to many variables, such as the selection of fishing site, time of year, mesh sizes, experience in handling and setting nets, and physical and chemical properties of the lake. Thus, it was only possible to conclude that fish in Hamell Lake could not be considered to be rare and that the total catch was perhaps below average when compared with other nearby lakes of lower heavy metal content.

Cliff Lake — Cliff Lake has a surface area of approximately 360 ha and a maximum depth of 11 m. The lake is the source of drinking water for the city of Flin Flon and because no power boats are allowed on the lake it is poorly fished. This lake had an average value for Zn of 85 $\mu g/\ell$ and a range, over the sampling period, of 70–120 $\mu g/\ell$. Copper averaged 10 $\mu g/\ell$ with a range of 9–11 $\mu g/\ell$ during the study. Zinc and copper concentrations at a series of five stations, including a vertical series and duplicate samples, ranged from 70 to 88 $\mu g/\ell$ and 9 to 11 $\mu g/\ell$, respectively, for a single sampling time.

The lake contained an abundance of fish. At least nine species were present; northern pike, walleye, lake whitefish, white sucker, yellow perch, lake herring (*Coregonus artedii*), burbot (*Lota lota*), trout-perch (*Percopsis omiscomaycus*), and spottail shiners (*Notropis hudsonius*). In general, there was no indication of year-class failure, abnormal growth, or abnormal reproductive impairment in any of the populations. Lake whitefish age 3–8 were common and the population appeared to contain slow- and fast-growing individuals. The occurrence of dwarf or slow-growing and fast-growing forms of whitefish has been described for other populations (Fenderson 1964). Some females were apparently not spawn-

TABLE 3. Comparison of catches among lakes. Catch per unit effort (CPUE) = number of fish divided by total length of gillnet set.

	Hamell Lake		Cliff Lake		Phantom Lake		Embury Lake	
Species	No.	CUPE	No.	CUPE	No.	CUPE	No.	CUPE
Walleye	8	.003	63	.025	—	—	—	—
Yellow perch	53	.002	155	.061	611	.873	14	.018
Northern pike	56	.023	45	.018	6	.009	9	.011
White sucker	53	.023	130	.051	15	.021	7	.009
Lake whitefish	29	.012	34	.013	—	—	14	.018
Other fishes	0	—	13	.004	48	.083	12	.015

ing each year. The failure of females from more northern populations to spawn each year has also been described for other populations of lake whitefish (Kennedy 1953). All northern pike age-classes from 2 to 9 were captured. Walleye were also large and ranged in age from 2 to 9 yr. Young-of-the-year yellow perch and lake herring up to age 6 were taken, as were all age-classes of immature white sucker. Mature white suckers older than 4 yr were not aged.

Other lakes — Lakes listed in this category were fished with less effort. Maximum depths are indicated when available.

Ross Lake was one of the smaller lakes fished (Fig. 1) but was a deeper lake with a maximum depth of approximately 9 m. Unlike other lakes fished that received heavy metals from atmospheric fallout, Ross Lake received toxicants directly from wastes entering from the inlet waters. Because of the extremely high concentrations of toxicants in the lake (Table 2), fish were unable to survive. However, the response of fish to the toxicant concentrations was interesting because of the accidental and intentional movement of some species into the high toxicant levels.

Local residents have reported that in the spring, white suckers move up the outlet of Ross Lake from the northwest arm of Schist Lake prior to spawning. In 1974, 99 white suckers, 11 lake herring, 4 northern pike, 2 walleye, and 1 lake whitefish were captured and tagged in this stream 500 m upstream of Schist Lake as part of a study being conducted by geologists from the Hudson's Bay Mining and Smelting Company (W. W. Fraser personal communication). In 1975, 24 northern pike and 132 white suckers were tagged. Flooding conditions in the creek apparently prevented the capture of all upstream migrants. Tagged and untagged white suckers were subsequently captured in Ross Lake. During the tagging period, toxicant concentrations (in micrograms per litre) averaged as follows: Ca, 210 in 1974 and 230 in 1975; Zn, 3550 in 1974 and 4970 in 1975; Fe, 690 in 1975; Pb, 120 in 1975; Cd, 50 in 1975; and Mn, 210 in 1975. The pH of the water was 6.3 in 1974 and 7.0 in 1975 (W. W. Fraser personal communication).

Gillnetting in the lake during the summer and fall in 1973 and 1974 resulted in the capture of 10 yellow perch and 1 northern pike. It is possible for fish to enter Ross Lake from other lakes and it is most probable that fish captured in the gill nets were migrants from other lakes and would either pass through or die in the lake. While this movement into the lake appeared accidental, the movement of white suckers up the inlet in the spring into such high heavy-metal concentrations was deliberate.

Embury Lake with Zn concentrations of 30–60 $\mu g/\ell$ is a moderately large deep lake (Fig. 1) with a maximum depth of 45 m. The lake contained lake trout (*Salvelinus namaycus*), burbot, white sucker, lake whitefish, yellow perch, northern pike, lake herring, and probably other smaller, less abundant species. Phantom Lake contains many shallow areas < 2 m but also contained a deeper area with a maximum depth of 10 m. The lake samples had Zn concentrations varying from 40 to 90 $\mu g/\ell$. Northern pike, lake herring, white sucker, and a large population of yellow perch were found in this lake. Douglas Lake, with Zn concentrations of 25–75 $\mu g/\ell$, contained yellow perch, northern pike, and white sucker. In an unnamed lake with a Zn concentration of 150 $\mu g/\ell$, identified as Lake No. 6 in this study, 14 pike and 1 white sucker were captured. Douglas Lake and Lake No. 6 were shallow lakes. No maximum depth estimate was available for these lakes.

Discussion

SOURCE OF HEAVY METALS IN THE LAKES

Elevated levels of heavy metals in lakes in an area such as Flin Flon can be caused by atmospheric fallout, liquid effluent discharge, and leaching of metal bearing minerals. Drainage

from the Flin Flon smelter is southward into Ross and Schist lakes. Of the lakes listed in Table 2, these latter are the only ones that could have been contaminated by liquid effluent from the smelter.

Koo and Mossman (1975) report economic ore bodies and "barren" sulfide deposits (combined Cu–Zn values $< 0.05\%$) are relatively common in the Flin Flon area. If the metal content of the water is resulting from leaching of metaliferous minerals, one would expect lakes with high Zn concentrations to be found scattered throughout the area. This is not the case. Many of the lakes, particularly those farthest from the smelter, have metal values similar to those of 109 relatively unpolluted lakes in northwestern Ontario (Beamish et al. 1976). The lakes with low metal content are those farthest from the smelter.

For the lakes other than Ross and Schist, a linear relationship was demonstrated between $\log_{10}$ Zn, Cu, and SO_4^{2-} concentrations and $\log_{10}$ distance from the smelter. This, coupled with the other conclusions reached above, suggests that the source of these substances is atmospheric fallout.

Effects of Heavy Metals on Fish

The problem of relating laboratory and field observations is well known (Brungs et al. 1976). It is difficult to determine the effect of above-normal but nonlethal concentrations of heavy metals. In particular it is difficult, on the basis of laboratory studies, to assess the effects of Zn concentrations in the 50–300 $\mu g/\ell$ range found in a number of the study lakes. Workers involved in the field of fish toxicology are generally careful not to try to predict what would happen under field conditions on the basis of laboratory tests. As a result, the problem of assessing the hazards of toxicants to fish populations is often passed on to the managers of an aquatic resource. This obviously is a very difficult task, as many problems must be considered, such as differing response among species, difference in water chemistry, difficulties in the analysis of toxicants in natural waters, and difference in the conditions of exposure as well as possible differences between the response of individual fish compared with the response of the populations.

In this present study, it was found that fish populations in lakes containing up to 90 $\mu g/\ell$ Zn and approximately 10 $\mu g/\ell$ Cu were not noticeably adversely affected by these heavy-metal concentrations. Fish in these lakes did not display abnormal growth, poor year-class strength, or unusually low abundance.

The response of fishes in Hamell Lake was more difficult to assess. A continued examination of this lake up to the fall of 1976 showed that mean annual concentrations of Zn remained at approximately 300 $\mu g/\ell$ (McFarlane and Franzine unpublished data). In 1976, concentrations as high as 1000 $\mu g/\ell$ were observed but these concentrations were found in the surface waters for only a short time in the early spring. During 1976 yellow perch and northern pike populations remained moderately abundant and continued to spawn; however, catches of white sucker, walleye, and lake whitefish were greatly reduced and spawning of white suckers appeared to be partially impaired.

Laboratory studies of the effects of Zn or Zn metal mixtures on fishes and other aquatic organisms have shown that harmful effects occur over the range of about 30–200 $\mu g/\ell$ (Brungs 1969; Biesinger and Christensen 1972; Eaton 1973). For example, fathead minnows (*Pimephales promelas*) exposed to approximate trimetal mixtures ranging from 40 to 300 $\mu g/\ell$ Zn, 7 to 30 $\mu g/\ell$ Cu, and 7 to 60 $\mu g/\ell$ Cd showed reduced spawnings and severe effects on reproductive performance beginning at a trimetal concentration of approximately 27 $\mu g/\ell$ Zn, 5 $\mu g/\ell$ Cu, and 4 $\mu g/\ell$ Cd (Eaton 1973). Much of the reproductive impairment was attributed to the presence of Zn. Our observations did not reveal any adverse effects on a variety of fish populations subjected to Zn and Cu concentrations of approximately 90 and 10 $\mu g/\ell$, respectively. Some long-term adverse effects occurred for some species that were subjected to Zn concentrations in the approximate range of 200–1000 $\mu g/\ell$ over a period of at least 4 yr. We cannot say that there has been no effect on the individual fishes and indeed, in Hamell Lake, adverse effects were apparent. However, many populations were surviving in high concentrations of Zn and, except where noted, if major changes were occurring in recruitment, growth, and survival of fishes or species composition in the lakes studied, then these changes were occurring over a time span of many years.

Acknowledgments

Mr W. W. Fraser from the Hudson's Bay Mining and Smelting Company, Flin Flon, Manitoba, kindly allowed us to quote the results of his unpublished tagging study from Ross Creek. The study could not have been completed without the competent technical assistance of Mr G. A. McFarlane and Mr B. Radziuk. Resources Research Company provided travel funds.

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Phytoplankton Production and Distribution in Howe Sound, British Columbia: A Coastal Marine Embayment–Fjord Under Stress

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Phytoplankton production and distribution were examined over a 2-yr period in relation to man-induced and natural factors that stress the system by mainly affecting the light regime in surface layer(s) of Howe Sound, British Columbia. Production rate and biomass values were greatest at the seaward boundary of the Sound where surface waters mix with the Strait of Georgia. Production decreases linearly in an up-inlet direction, reaching minimum values at the head of the Sound where the influence of the turbid Squamish River discharge is greatest. Annual production in the boundary waters of the Sound for 1973 and 1974 was 300 and 516 g $C \cdot m^{-2}$, compared to an average of 118 and 163 for remaining stations. Strong light attenuation by the turbid Squamish River and flushing by the seaward moving surface layer were considered the most important factors controlling phytoplankton production and distribution in Howe Sound. Colored effluent from two pulp mills and turbid mine tailings and gravel washing water were minor perturbants to the system as a whole, but in affected bays and subregions of the Sound their effects on phytoplankton production were considerable. Annual production in Howe Sound was slightly higher than values for the Strait of Georgia and considerably greater than estimates from the North Pacific.

Key words: phytoplankton, production, fjord–embayment, coastal marine, phytoplankton distribution, succession

STOCKNER, J. G., D. D. CLIFF, AND D. B. BUCHANAN. 1977. Phytoplankton production and distribution in Howe Sound, British Columbia: a coastal marine embayment–fjord under stress. J. Fish. Res. Board Can. 34: 907–917.

Les auteurs ont étudié la production et la distribution du phytoplancton sur une période de 2 ans en relation avec des facteurs tant naturels que dus à l'homme imposant des contraintes au système, surtout par leurs effets sur le régime lumineux dans la ou les couches superficielles du détroit de Howe, Colombie-Britannique. Le taux de production et les valeurs de la biomasse sont à leur maximum à la limite entre le détroit et la mer, où les eaux de surface se mélangent à celles du détroit de Georgie. La production diminue de façon linéaire à mesure qu'on remonte l'inlet, atteignant des valeurs minimales à la tête du détroit de Howe, où l'influence des eaux turbides de la rivière Squamish est maximale. La production annuelle dans les eaux limites du détroit en 1973 et 1974 était de 300 et 516 g $C \cdot m^{-2}$, comparée à une moyenne de 118 et 163 aux autres stations. Une forte atténuation de la lumière par les eaux turbides de la rivière Squamish et la chasse d'eau par la couche superficielle se déplaçant vers la mer sont considérées comme les facteurs les plus importants dans le contrôle de la production et de la distribution du phytoplancton dans le détroit de Howe. L'effluent coloré de deux moulins de pâte à papier, des déchets de mines et l'eau turbide de lavage du gravier sont des agents mineurs de dérangement du système dans son ensemble, mais dans les baies et sous-régions affectées du détroit, leurs effets sur la production du phytoplancton sont considérables. La production annuelle dans le détroit de Howe est légèrement plus élevée que les valeurs obtenues dans le détroit de Georgie et est considérablement plus grande que les estimés pour le Pacifique Nord.

Received May 31, 1976
Accepted February 15, 1977

Reçu le 31 mai 1976
Accepté le 15 février 1977

Printed in Canada (J4375)
Imprimé au Canada (J4375)

FACTORS influencing marine phytoplankton production and distribution in British Columbia inlets are poorly understood. As interest focuses on potential industrial development of estuaries and tidal marshes located in the numerous inlets along Canada's coastline, it becomes important to document factors that influence the primary formation of organic matter in these inlets, and how their phytoplankton populations react to stress, either natural or man-induced. There is now an increasing awareness of the importance of the vernal phytoplankton bloom and its relationship to all other components of the marine food web. Barnes (1957) and Himmelman (1975) have demonstrated the relation between invertebrate spawning, resultant larval success, and timing of the spring bloom, while Parsons (1965) and other workers have suggested that the year-class strength of certain salmonid populations relates closely to timing of the vernal phytoplankton bloom in the Strait of Georgia.

Howe Sound is situated close to Vancouver, B.C., and receives effluent discharges from two kraft process pulp mills, and up to spring 1975, mine tailings from the Britannia copper mine and from several gravel operations. The Sound is also strongly influenced by discharge of the large, glacially turbid Squamish River. Past studies in Howe Sound have been largely physical (Carter 1934; Pickard 1961), geological (Mathews and Murray 1966), and chemical (Waldichuk et al. 1968). No detailed biological oceanographic work was performed prior to 1972, when the Plankton Ecology group of the Pacific Environment Institute commenced studies on the pelagic communities of Howe Sound.

The objectives of this work were: (1) to describe the seasonal succession and distribution of phytoplankton, (2) to identify factors influencing phytoplankton production, (3) to assess the impact that natural and man-induced stresses have on the annual formation of organic matter, and (4) to relate daily and annual production rates in Howe Sound to adjacent coastal waters, other British Columbia inlets, and to similar waterbodies located throughout the world. The former three objectives enabled one of us (D.B.B.) to develop a sufficient data base to mathematically model the primary and secondary levels of the Howe Sound plankton community (Buchanan and Stockner 1976).

Materials and Methods

Carter (1934) considered Howe Sound to be a combined fjord and coastal embayment, the fjord portion extending from Anvil Island north to the Squamish River estuary (Fig. 1). The Squamish

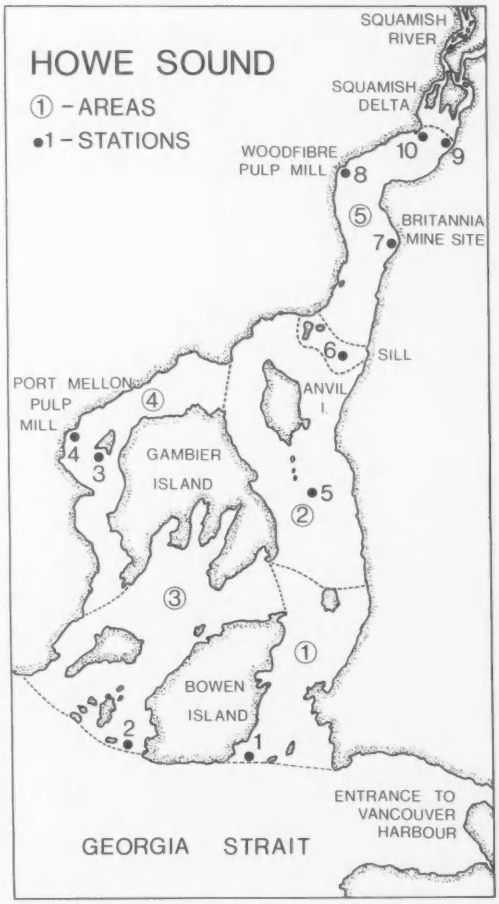

FIG. 1. Howe Sound with station locations (●) and zones (○) referred to in text.

River discharge influences all of Howe Sound, particularly the center channel which includes Areas 5, 2, and 1 (Fig. 1). From May to September the river carries a heavy glacial silt load which forms an opaque, freshwater lens on the surface of Howe Sound. Because rainfall is heavy (approximately 221 cm annually), and mean river discharge is large ($\bar{x}$ = 242 $m^3 \cdot s^{-1}$), Howe Sound is considered a positive estuary, where precipitation and runoff greatly exceed evaporation, resulting in a net seaward water flow. A brief description of Howe Sound estuarine circulation is given by Giovando (1972). Although Howe Sound is a multilayered system, it is the surface layers (euphotic zone) that are of importance in this study. Tides in Howe Sound are typical of the Pacific coast, being of the mixed type with a large diurnal inequality between the magnitude and timing of highs. The mean range is 3.2 m with a maximum of 5.0 m.

Ten sampling locations were selected in Howe Sound (Fig. 1). The Sound was further divided on the basis of known morphometric and associated physical characteristics into five zones. Stations 1 and 2 at the entrance of Howe Sound monitored the boundary areas where surface Howe Sound and Strait of Georgia waters mix. Station 3, located off the southern tip of Woolridge Island, served as a control for Station 4, located adjacent to Port Mellon pulp mill. These stations were situated in Thornbrough Channel and were not strongly influenced by the surface seaward movement of Squamish River water. Stations 5 and 6 in the midreaches of Howe Sound were in the main channel, Station 6 positioned on the Howe Sound sill (90 m depth), and Station 5 off Pam Rock at the southern tip of Anvil Island. Stations 7 and 8 were adjacent to Britannia copper mine and Woodfibre kraft pulp mill and monitored these stress points. Stations 9 and 10 were located directly off the Squamish estuary and were both strongly influenced by the Squamish River discharge.

Total incident solar radiation (joules per square centimetre) was recorded on a Belfort pyrheliometer. Extinction of surface light with depth was measured by a Montedoro-Whitney and Inter Ocean Underwater Illuminance meters (Models LMT-8A and 510). Light data were plotted on a Hewlett-Packard Calculator Plotter as a function of depth, and a line was regressed through the points whose slope gave the mean extinction coefficient, k. Intensity of surface radiation in lux units was measured by a Gossen handheld light meter. A standard 30 cm white Secchi disc was used to measure water transparency at every set. In measuring light penetration adjacent to pulp mills, special care was taken to drift onto the station so as not to disturb the surface stain.

Temperature profiles to a depth of 60 m were obtained with a bathythermograph (BT). A bucket thermometer was used to measure surface temperatures for BT calibration.

Water samples were collected from 1-, 3-, 5-, and 20-m depths. From each depth, 100 ml of water was stored in acid-rinsed polyethylene bottles and analyzed for inorganic carbonate carbon with an Orion digital pH meter (Model 801), and the method of Strickland and Parsons (1968) to determine carbonate alkalinity. However, if after acid addition final pH values fell below 3.00, then the sample titration was repeated using APHA et al. (1971) standard titriometric methods.

Samples from the same depths were analyzed with an Auto-Lab salinometer (Model 601) to an accuracy of ±5%. Density was computed by nomograph from temperature and salinity records.

Dissolved oxygen values (1, 3, 5, and 20 m) were determined by the Winkler titration method (Strickland and Parsons 1968). Standard 250-ml glass stoppered BOD bottles were fixed within an hour of being taken and oxygen was determined the same day.

Samples for nutrient analysis were obtained from 1-, 5-, and 20-m depths, and immediately frozen. Samples were analyzed by the Fisheries/Environmental Protection Service analytical laboratories, Pacific Environment Institute, West Vancouver. Methods used are as outlined in their manual (Fisheries/EPS 1974).

The standard ^{14}C method as initially proposed by Steeman Nielsen (1952) was used with some minor modifications incorporated. Water was collected from surface skim, 0.5-, 1-, 2-, 3-, 5-, 10-, 20-, and 30-m depths using a 6-ℓ polyvinylchloride Van Dorn bottle. Productivity bottles (two 125 ml light and one 125 ml dark) were inoculated with 1 ml $NaH^{14}CO_3$ radioisotope stock (ca. 1 $\mu Ci \cdot ml^{-1}$), using an automatic pipette. For each experiment, the number of dpm's per millilitre was determined by placing 1 ml in each of three scintillation vials. Samples were usually incubated for 4–5 h, normally from 0930 to 1430. Water was filtered through a 0.45-μm Sartorius cellulose nitrate filter, and after rinsing, filters were placed in 10 ml of a specially prepared toluene based fluor (POPOP, PPO, 2-ethoxyethanol, and toluene). Samples were analyzed for activity in a Packard Tri-Carb Liquid Scintillation Spectrometer (Model 3375). The equation of Strickland (1960) was used to convert dpm's to milligrams of carbon per cubic metre. Profiles were integrated by a Hewlett-Packard Calculator Plotter (Model 9820A) to give phytoplankton production on an areal basis (milligrams of carbon per square metre per day).

Phytoplankton samples from 1- and 5-m depths were examined to assess species composition, dominance of major taxa, and phytoplankton volumes during key spring and fall bloom periods. Phytoplankton samples were preserved in Lugol's solution and enumerated by equating phytoplankton cells to known geometric shapes. Each phytoplankton sample was examined under 175 and 700× magnification using a Wild M40 inverted plankton microscope. Results were expressed as cells and total volume per cubic metre.

One litre of seawater was taken from 1-, 3-, 5-, and 20-m depths for chlorophyll a analysis and filtered onto Whatman GF/C glass fiber filters with a small amount of $MgCO_3$ added to prevent acidification of filters with freezing. Filters were macerated in a tissue grinder with 10 ml of 90% acetone, and the filtrate was analyzed on a Cary recording spectrophotometer (Model 15) for chlorophyll a. Amounts were calculated using the SCOR-UNESCO equation given in Strickland and Parsons (1968).

Vertical zooplankton hauls from 50 m to the surface were made at each station with a SCOR-UNESCO plankton net, with mouth diameter of 57 cm and screen mesh size of 350 μm. Samples were preserved in 5% Formalin, returned to the laboratory, and split into two equal subsamples. Zooplankton volume was determined from one portion in an Imhoff cone, and the other portion was filtered onto a preweighed GF/C filter and dried to constant weight at 90°C. After dry weight determination they were placed in a muffle furnace at 500°C for 4 h to obtain estimates of ash-free dry weight. Values are expressed as millilitres per cubic metre and milligrams per cubic metre.

A mathematical model of phytoplankton population

TABLE 1. Maximum–minimum values and annual means of selected physical, chemical, and biological variables in the surface layer (0–20 m) of Howe Sound in 1973 and 1974.

Stn./ Yr.	Temp. (°C)	Salinity ($^{oo}/_{oo}$)	Density (σt)	Dissolved O_2 ($mg \cdot \ell^{-1}$)	TNO_3-N ($mg \cdot \ell^{-1}$)	TPO_4-P ($mg \cdot \ell^{-1}$)	SiO_2 as Si ($mg \cdot \ell^{-1}$)	k	Chl a ($mg \cdot m^{-2}$)	Primary product· ($g\ C \cdot m^{-2} y \cdot r^{-1}$)
1										
1973	(11.0)	(22.68)	(16.96)	(6.72)	(.127)	(.045)	(1.05)	(.36)	(24.6)	
	6.6–16.2	13.03–27.25	9.09–21.20	5.89–8.57	.010–.343	.012–.075	.71–1.48	.27– .69	0– 88.3	299
1974	(10.3)	(21.08)	(17.00)	(7.31)	(.178)	(.060)	(1.14)	(.63)	(41.2)	
	6.0–18.0	11.69–27.05	12.00–21.26	6.10–9.11	.010–.385	.041–.073	.62–1.55	.23–1.33	0–120.3	516
2										
1973	(11.7)	(22.07)	(16.78)	(6.87)	(.104)	(.032)	(.91)	(.38)	(22.9)	
	6.2–16.2	15.39–27.88	12.22–21.68	5.62–8.13	.013–.330	.013–.056	.74–1.11	.24– .60	2.3– 77.8	170
1974	(10.1)	(22.60)	(18.19)	(7.34)	(.176)	(.047)	(1.06)	(.41)	(45.0)	
	5.5–17.0	12.84–28.12	12.84–22.05	6.35–8.77	.010–.368	.014–.071	.41–1.56	.21– .77	0.1–157.4	438
3										
1973	(10.9)	(22.14)	(17.27)	(6.69)	(.138)	(.053)	(1.01)	(.42)	(19.7)	
	6.3–16.4	15.35–26.55	11.45–20.73	5.54–9.34	.010–.370	.021–.086	.69–1.36	.26–1.06	0.4–83.7	112
1974	(10.5)	(21.22)	(16.16)	(7.18)	(.147)	(.048)	(.87)	(.40)	(17.9)	
	4.6–16.3	14.40–27.12	10.46–21.49	6.03–9.59	.013–.333	.015–.065	.25–1.65	.23– .60	4.0–47.1	130
4										
1973	(11.3)	(21.43)	(15.81)	(6.54)	(.128)	(.050)	(1.02)	(1.65)	(11.9)	
	6.6–16.8	14.57–26.99	10.70–20.59	5.13–9.14	.008–.345	.019–.080	.72–1.49	.47–3.11	0.4–60.0	10
1974	(10.1)	(21.30)	(16.37)	(6.78)	(.079)	(.048)	(.90)	(2.37)	(15.3)	
	4.8–16.1	13.55–26.72	10.18–21.41	5.81–9.07	.010–.250	.015–.071	.25–1.62	.68–5.30	0.6–45.7	15
5										
1973	(10.1)	(22.83)	(17.25)	(7.20)	(.069)	(.055)	—	(.45)	(11.9)	
	6.3–13.8	15.53–27.19	11.52–21.38	6.43–8.65	.010–.168	.026–.079	—	.18– .87	2.7–29.3	142
1974	(10.4)	(20.24)	(15.35)	(7.39)	(.163)	(.049)	(1.01)	(.34)	(18.0)	
	4.5–15.1	13.62–29.52	9.85–20.49	5.30–9.63	.010–.350	.013–.070	.18–1.66	.20–.54	1.4–47.4	181
6										
1973	(10.6)	(22.24)	(17.06)	(7.50)	(.059)	(.051)	—	(.41)	(13.5)	
	6.2–15.3	18.18–26.52	13.70–20.87	6.79–8.89	.010–.171	.010–.075	—	.28–.54	2.8–35.1	85
1974	(9.5)	(19.83)	(15.40)	(7.36)	(.194)	(.046)	(1.06)	(.49)	(13.1)	
	4.4–14.0	11.34–26.07	9.16–20.63	5.88–9.36	.017–.344	.018–.066	.25–1.64	.20–1.01	0.5–44.3	109
7										
1973	(10.9)	(24.19)	(17.50)	(6.55)	(.139)	(.051)	(1.03)	(.50)	(10.9)	
	6.7–15.2	16.86–29.16	12.49–21.33	5.48–9.27	.020–.303	.017–.076	.42–1.48	.24– .82	0.1–78.6	69
1974	(8.8)	(21.73)	(16.74)	(6.53)	(.158)	(.050)	(1.02)	(1.02)	(14.4)	
	5.3–14.6	10.87–26.25	7.96–20.00	5.67–8.14	.013–.295	.024–.073	.28–1.75	.30–2.64	0.7–41.1	103
8										
1973	(9.8)	(20.80)	(15.53)	(6.71)	(.120)	(.058)	(1.08)	(1.00)	(14.1)	
	5.9–13.9	11.66–27.87	8.79–19.86	5.45–9.22	.013–.277	.020–.089	.55–1.67	.62–1.56	0.3–92.1	42
1974	(8.4)	(19.76)	(15.34)	(6.39)	(.125)	(.055)	(.98)	(1.71)	(7.8)	
	4.8–12.5	10.87–25.53	8.74–20.10	5.71–7.25	.027–.207	.036–.092	.45–1.50	.97–2.10	1.2–18.1	37
9										
1973	(9.5)	(22.31)	(15.72)	(6.67)	(.141)	(.052)	(1.07)	(.81)	(11.1)	
	5.9–13.7	6.67–29.69	4.79–20.82	5.19–11.34	.010–.307	.026– .80	.76–1.44	.19–1.89	0–124.0	76
1974	(8.5)	(20.25)	(15.67)	(6.47)	(.192)	(.046)	(1.33)	(.59)	(8.2)	
	5.0–12.9	5.77–26.29	4.25–20.25	4.88–8.15	.020–.361	.012–.071	.50–2.02	.19–1.85	0.4–14.2	69
10										
1973	(8.8)	(22.15)	(15.78)	(6.86)	(.120)	(.062)	(1.00)	(.78)	(12.1)	
	5.2–12.6	7.00–29.75	5.11–20.56	5.34–11.24	.010–.300	.033–.095	.74–1.52	.26–2.76	0.3–116.2	108
1974	(7.8)	(19.13)	(14.82)	(6.71)	(.203)	(.046)	(1.42)	(1.23)	(9.3)	
	4.5–12.1	7.83–23.88	5.85–18.66	4.83–8.17	.039–.393	.021–.066	.68–2.02	.32–2.99	1.0–22.1	57

growth and distribution was developed for Howe Sound. Details are presented elsewhere (Buchanan and Stockner 1976).

Results

PHYSICOCHEMICAL PARAMETERS

At all stations for all years, monthly surface temperatures paralleled air temperature variation, reaching highest values in July and August and lowest in January and February. These peak values were approximately 2 mo behind the peak of surface irradiation, indicating integral solar heating in the stratified surface layers at this time. Surface temperatures in summer tended to be highest at Station 1, and progressively cooler up-inlet at stations under the influence of Squamish River discharge (Table 1). Temperatures at 20 m were spatially variable in summer, depending on mixed layer depth, and seasonally were considerably colder than surface values.

Thermal stratification commences in early April, becomes pronounced in summer, and is destroyed by complete mixing in November. At the entrances to Howe Sound (Queen Charlotte and Collingwood channels), throughout much of the summer a single thermocline occurs between 5 and 7 m deep (Stations 1 and 2), while from sill to river mouth (Stations 6–10) a double thermocline is common, as cold Squamish River water overlies and is entrained with the warmer surface layer of Howe Sound. The depth of the surface lens of river water varies from 0.5 to 2 m, depending on tide, wind, and river discharge velocity.

In the surface layer salinity was seasonally and spatially variable, depending largely on the stage of the Squamish River discharge. Lowest values in surface layers occurred in June or July, with highest values noted at all stations in January and February (Table 1). Generally, in summer, surface salinities at Stations 1 and 2 were higher

than those up-inlet under Squamish River influence, but there was considerable month to month variation.

A halocline occurs throughout the year, generally very shallow and weak in winter, and deepening and becoming more pronounced in May–June as the surface layer is influenced by outflow from the Squamish system. The halocline varied in depth from 5 to 7 m throughout the summer at all stations up to the sill. From the sill to the estuary a double halocline existed throughout much of the summer, similar in characteristics to the double thermocline previously described.

Variations in density were similar to those just described for salinity and temperature. Highest values were in January at all stations, and lowest in May (Table 1). Highest average values were at Station 1 in Queen Charlotte Channel and lowest average values were at Station 10, off the Squamish River mouth. Pycnocline formation, seasonal depth variation, and structure were similar to halocline and thermocline variation previously described.

At all stations for each year dissolved oxygen values in the surface layer (0–5 m) showed similar seasonal trends, with peak values coincident with greatest phytoplankton biomass (Table 1). At 20 m deep, values were similar at all stations in all years with highest values in late winter and early spring and lows in October–November.

Values of carbonate carbon varied seasonally in parallel with the extended duration of freshwater influence upon the surface layer (Table 1). Lowest values coincided with lowest salinities during river freshet periods, ranging from lows of 6×10^3 mg $C \cdot \ell^{-1}$ at Station 10 in July to a high of 20×10^3 at Station 2 in the same period. Values at 20 m were seasonally stable, ranging from 20×10^3 to 25×10^3 mg $C \cdot \ell^{-1}$.

Incident radiation showed typical temperate latitude seasonal variation with typical summer values ranging from 2427 to 2720 $J \cdot cm^{-2} \cdot day^{-1}$ and winter lows of 41.8 to 314. Stations 7–10 in the fjord portion of Howe Sound receive less daily radiation because of high surrounding mountains and greater cloud cover (Table 1).

Greatest light penetration occurred at the entrances to Howe Sound (Stations 1 and 2), where mean extinction coefficients (k) were 0.44 and 0.37, compared to 0.65 and 0.87 at Stations 9 and 10 in the outer Squamish estuary (Table 1). Seasonally, mean Secchi depth values showed trends similar to those for k. Waters adjacent to pulpmills and mines (Stations 4, 7, and 8) showed reduced clarity as depicted by low Secchi and high extinction values.

Seasonal trends in extinction and Secchi were correlated with the seasonal cycle of plankton in surface layers from April to June and with Squamish River freshet from June to September. By comparing the 1% light isoclines at Station 3 in July, affected mainly by autochthonous matter, with those of Station 10 in the Squamish estuary during approximately the same period, the relative magnitude of Squamish River influence on light penetration can be assessed (Fig. 2).

Winter values of nitrate, phosphate, and silicate showed uniform concentrations with depth in all years. Nitrate was reduced to undetectable levels at most stations, just preceding the peak of the vernal phytoplankton bloom (Table 1, Fig. 3). Phosphate and silicate concentrations remained high throughout the year, showing some minor decreases in spring and late summer. Depending on wind and tide, entrainment of nitrate into surface layers occurred at Stations 1 and 2 at the mouth of Howe Sound in summer, but at other stations nutrient values remained low until complete mixing restored concentrations to typical high winter levels in November–December (Fig. 3). Concentration of the three nutrients were

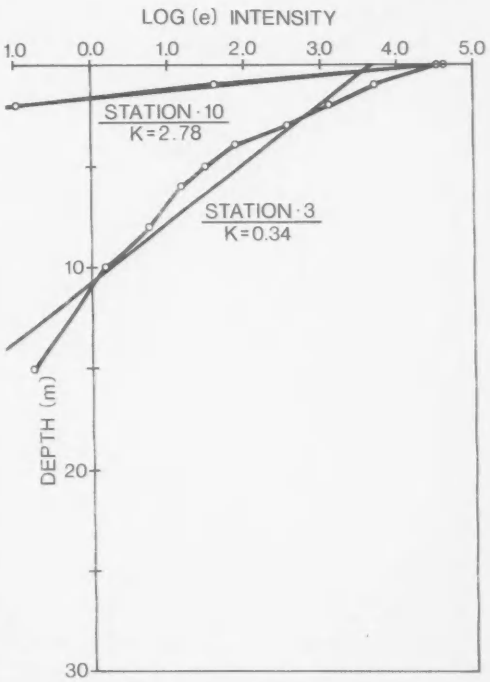

FIG. 2. Plot of light extinction coefficients (k) with depth at Station 3 on July 12, and Station 10 on June 27, 1973.

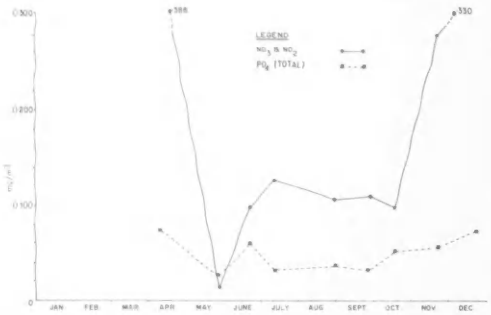

FIG. 3. Annual variation in concentrations of nitrate-nitrite and total phosphate at Station 3 in the surface layer (0–5 m). The pattern shown is representative of nutrient conditions at most stations in Howe Sound.

high and relatively stable throughout the year at a depth of 20 m. Waters affected by the two pulp mills (Stations 4 and 8) in summer showed slightly elevated concentrations of nitrate and phosphate.

BIOLOGICAL VARIABLES

The phytoplankton community of Howe Sound was composed of six major groups: diatoms, dinoflagellates, cryptophytes, silicoflagellates, chrysophytes, and euglenophytes. In total, there were 44 diatom species, 18 dinoflagellates, and a number of miscellaneous species (For a detailed taxonomic description see Stockner and Cliff 1976). Of the total number of species, 19 were classified as major taxa, and 50 as minor.

Dominant species in Howe Sound were all diatoms: *Skeletonema costatum*, *Thalassiosira aestivalis*, *T. nordenskioldii*, *T. pacifica*, and *Chaetoceros* spp., with *S. costatum* and *T. pacifica* dominants at all stations. A number of freshwater species were observed at stations near the head of the inlet; these included *Asterionella formosa*, *Hannaea arcus*, *Meridion circulare*, *Eunotia* sp., *Stauroneis* sp., and *Tabellaria flocculosa*. Species composition and population density at Stations 1–5, in the seaward region of the Sound, were different from those at Stations 6–10, in the inner region of the Sound.

Phytoplankton volumes at 1 m deep were partitioned to show the seasonal contribution of dominant species to total volume at each station (Fig. 4). There was no clear predictable pattern of species succession in Howe Sound. In 1973 *Thalassiosira* spp. were the vernal bloom dominants at most stations, but in 1974 it was *Skeletonema costatum*. At stations where a fall increase occurred, it was largely dominated by the diatoms *Chaetoceros* spp. and *S. costatum*. The most important dinoflagellates were *Glenodinium* sp. and *Gymnodinium* sp., attaining maximum abundance in early autumn, but representing only 10% of the total phytoplankton volume at this time. Many species of euglenophytes, cryptophytes, and chrysophytes were present throughout the growing season, but they never comprised more than 2–3% of the total phytoplankton volume.

Biomass and numbers of phytoplankton in Howe Sound showed wide seasonal and spatial variation (Fig. 4). Vernal peaks were distinct at all stations, but autumnal peaks of any significance occurred only at more seaward locations (Stations 1–5). Phytoplankton biomass at 1 m deep was consistently greater than at 5 m. For purposes of comparison, phytoplankton volumes from both depths were integrated and results showed significantly greater amounts of plankton at Stations 1–5 than at Stations 6–10 ($t = 3.67$, $df = 8$, $P > 0.01$). Greatest mean phytoplankton densities and biomass occurred at Stations 1 and 2 at the mouth of the Sound.

Chlorophyll *a* showed time and space variations similar to those just discussed for phytoplankton (Fig. 5). Greatest amounts of chlorophyll *a* occurred in boundary waters of the Sound, with least amounts in waters adjacent to pulp mills, the Britannia copper mine, and off the Squamish estuary (Table 1). Peaks coincided with vernal and autumnal phytoplankton blooms, but showed slight phase lags with productivity values.

Primary production was highest in April–May at all stations, with pronounced peaks at up-inlet stations prior to Squamish River freshet and more prolonged multiple peaks at the head of the Sound (Fig. 6). After commencement of Squamish River freshet, production at up-inlet stations fell sharply and remained low for the remainder of the growing season. Daily production rates ranged from highs of just over 5 g $C \cdot m^{-2}$ in July at Station 1 to lows of 40–50 mg $C \cdot m^{-2}$ in July at Stations 9 and 10, with summer averages of 0.5–0.7 g $C \cdot m^{-2}$ at midchannel locations (Stations 5–6). Mean daily production rates in waters adjacent to pulp mills (Stations 4 and 8) were consistently lower than most stations in the Sound, and values from waters affected by Britannia mine discharges (Station 7) were intermediate (Fig. 7).

On an annual and daily basis, primary production in boundary waters (Stations 1 and 2) was consistently higher than other Howe Sound stations. With the exception of stations adjacent to the pulp mills, there was an obvious trend of

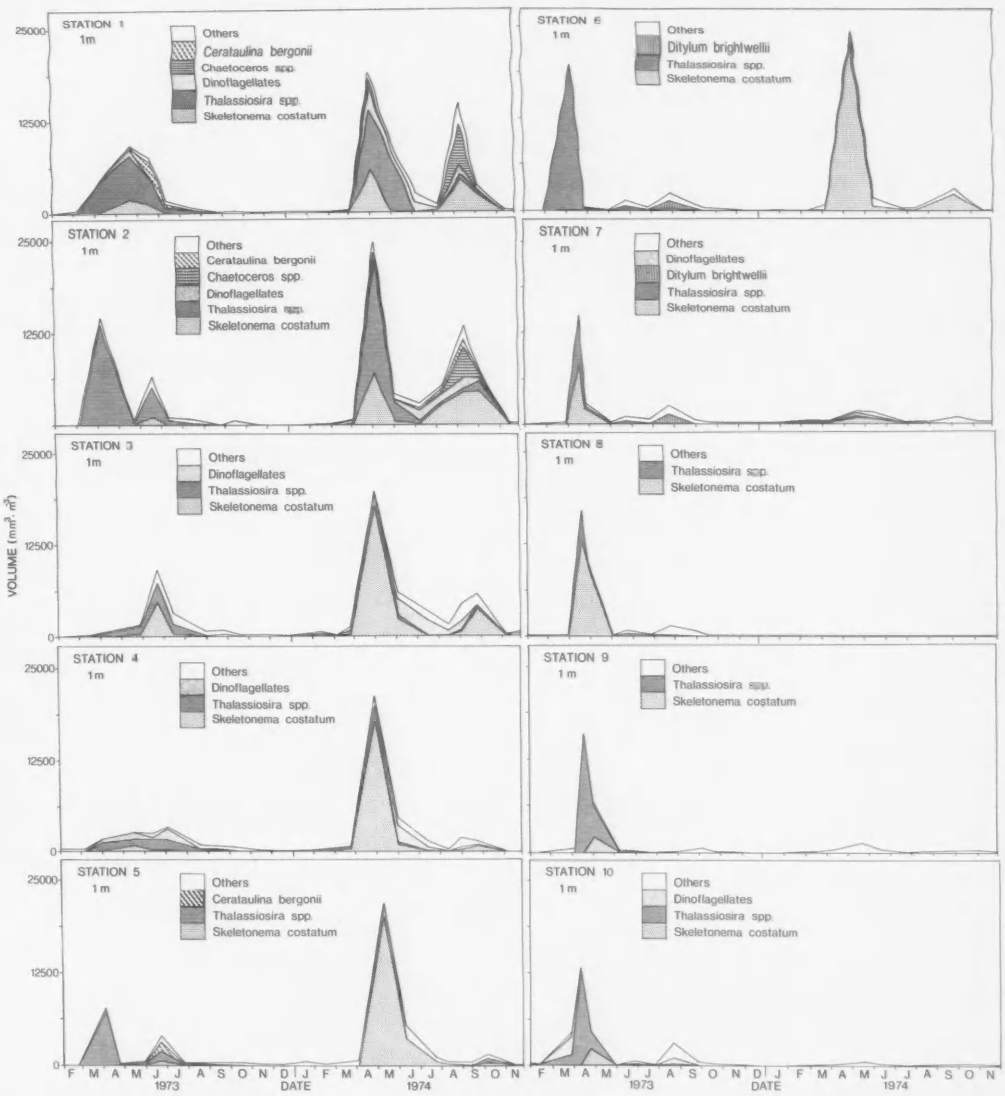

FIG. 4. Total phytoplankton volume at 1 m deep at Stations 1–10 in Howe Sound in 1973 and 1974, partitioned into abundance by dominant species.

diminishing production in an up-inlet direction (Table 1, Fig. 7). When light ($\bar{x}\ k$) and ln transformed production estimates listed in Table 1 for both years for the 10 stations in Howe Sound were regressed, the correlation coefficient ($n = 20$, df $= 19$, $r = 0.79$) was significant at the $P = 0.01$ level, emphasizing the strong influence of light on primary production in Howe Sound.

One zooplankton vertical haul at each sampling interval led to the wide time and space variations among stations (Table 1). The only consistent pattern seen from these data was that peak abundances occurred in May and June of both years, with a phase lag of several weeks between successive zooplankton and phytoplankton population peaks.

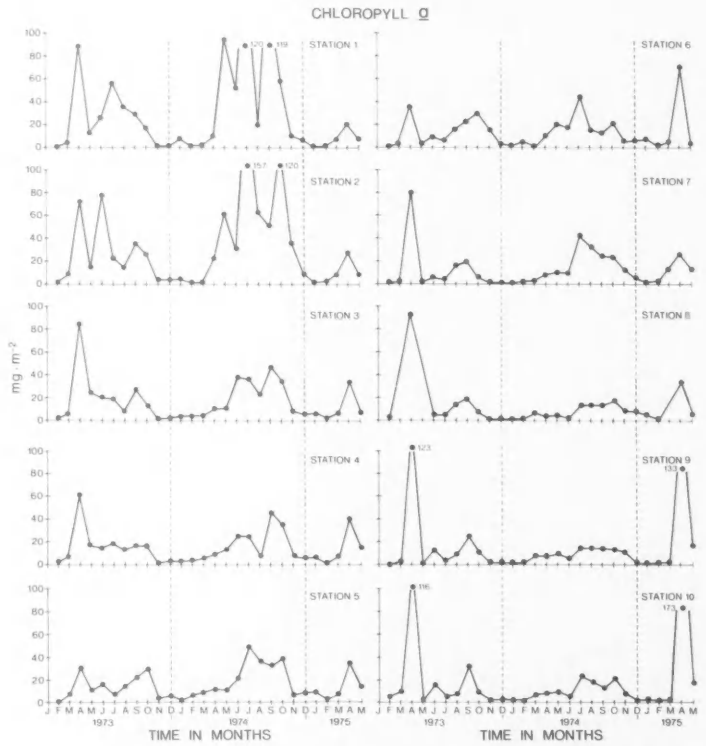

FIG. 5. Integral chlorophyll *a* values (0–20 m) at Stations 1–10 in Howe Sound in 1973 and 1974.

Discussion

Publications by Carter (1933) and LeBrasseur (1954) indicated that British Columbia inlets were generally "plankton poor" in their main body and "plankton rich" in the vicinity of their mouth. Our current Howe Sound results agree with this general description. The pronounced spatial distribution pattern of phytoplankton biomass and production in Howe Sound is largely due to the strong influence of the turbid Squamish River discharge and the accompanying variation in chemical and physical properties that it imparts to the surface layers. In April and early May, phytoplankton populations significantly increase in all regions of Howe Sound; however, as the Squamish River reaches maximum discharge in June, a large portion of phytoplankton biomass at the head of the inlet is gradually flushed seaward, and the opaque, brackish surface layer prevalent throughout the summer severely limits phytoplankton growth in the upper reaches of Howe Sound and rates of export and sinking greatly exceed production. This process is nicely illustrated in data from successive cruises to Station 10 in April and May of 1973, where despite a doubling in incident radiation, strong attenuation of light by the surface layer and rapid seaward flushing reduced production to negligible values (Fig. 8). By September, with the gradual disappearance of the surface turbid layer, incident light and surface layer temperatures were too low to stimulate significant phytoplankton growth. Consequently, autumnal increases of phytoplankton stocks in these regions of the Sound were small. Some replenishment of export losses by viable cells moving up-inlet in the deeper, more saline layer may occur, but the probability of renewed growth in the surface layers affected by Squamish River turbidity are small. The strong seaward movement of the surface layer (6–8 $km \cdot day^{-1}$) (Bell 1975), coupled with poor light attenuation and low temperatures, are responsible for the paucity of phytoplankton stocks and low growth seen at Stations 9 and 10 at the head of the inlet.

In contrast, phytoplankton transported to the boundary waters of the Sound are likely to exhibit continued growth in the more favorable light and nutrient regime found here. Because of

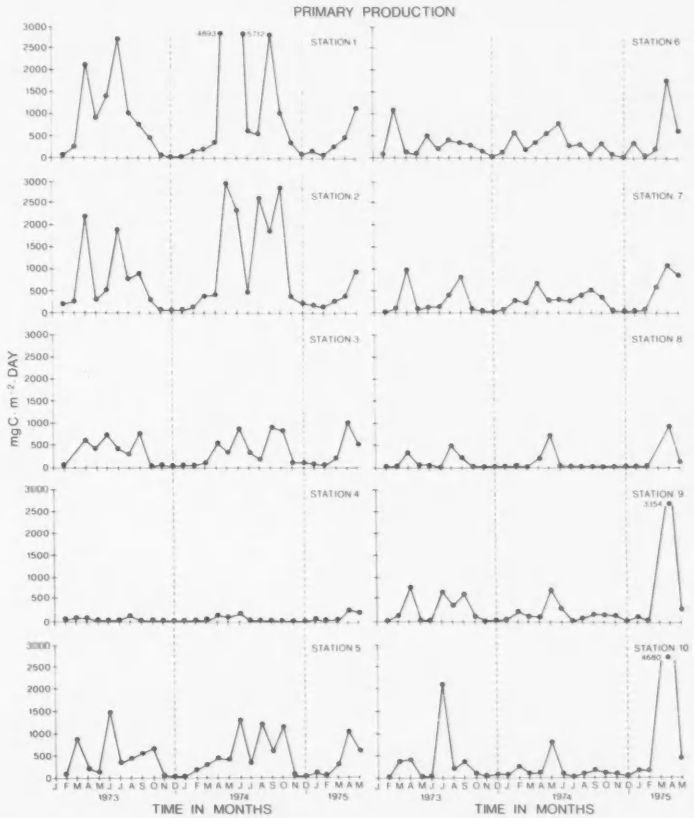

FIG. 6. Daily integral rates of primary production at Stations 1–10 in Howe Sound in 1973 and 1974.

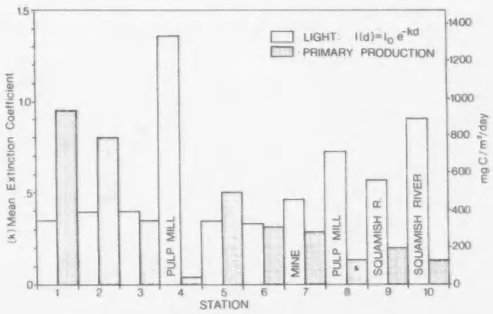

FIG. 7. Relation of mean light extinction and mean production rate for Stations 1–10 in Howe Sound in 1973.

the open exposure to winds of considerable force, the mixed layer is less stable, more turbulent, and more variable here (Waldichuk 1957), all factors which contribute to nutrient recharge in the euphotic zone in boundary waters of Howe Sound. It is primarily for these reasons that primary production is so high and phytoplankton standing stock so large at Stations 1 and 2. This type of positive estuarine circulation imparts to all British Columbia embayments with turbid outflows the characteristic phytoplankton production and distribution gradients from head to seaward boundary typified by Howe Sound data (Fig. 7) and discussed for other British Columbia coastal embayments by Hutchinson and Lucas (1931), Carter (1934), and LeBrasseur (1954).

Commencement of the spring bloom in Howe Sound is related to high nutrients, increased incident radiation, and the onset of thermal stratification in April and May. Self-shading is an important feedback on the system at this time, while later in the year, light attenuation depends more on river derived particulates (Buchanan and Stockner 1976). The spring bloom in Howe Sound in 1974 was much later than in 1973, largely because of poor spring weather conditions

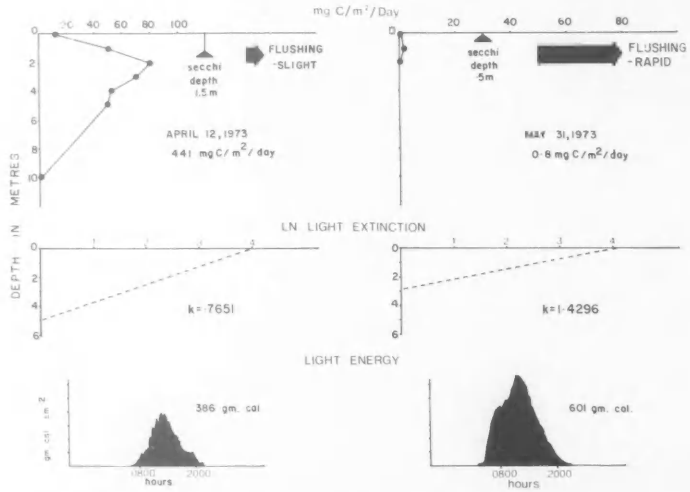

FIG. 8. The relation between light and production at Station 10, Howe Sound on April 12, 1973 during low Squamish River discharge and on May 31, 1973 during maximum river discharge.

that year. Consequently, the spring bloom at the head of Howe Sound, which normally occurs in mid-April, was virtually negated in 1974 by the Squamish River freshet, which created poor subsurface light conditions at the onset of what would normally have been the maximum growth period. Thus, in lower British Columbia coastal marine waters, the commencement of the vernal bloom can occur as early as mid-March, or be delayed by poor spring light conditions until mid-May. The greater the delay, the more likely the suppression of phytoplankton growth by turbid water conditions in surface waters at the head of inlets with glacial outflows (Buchanan and Stockner 1976).

Working in an embayment (Indian Arm) close to Howe Sound with a less turbid river discharge, Buchanan (1966) observed phytoplankton to be most diverse during the period June to September. This observation agrees with our Howe Sound results, which show one or often two species dominant during the spring bloom period. (*S. costatum* and *Thalassiosira* spp.), and many species of rather equal population size present during the summer at more seaward stations. Just as rates of production were concluded to be dependent upon a number of factors, similarly, phytoplankton species diversity and biomass variations in Howe Sound are considered to be dependent more on a combination of factors, the most important of which are light attenuation and physical transport (flushing) (Stockner and Cliff 1976; Buchanan and Stockner 1976).

From our study four factors were identified as indirectly affecting phytoplankton growth in Howe Sound: the turbid Squamish River discharge, two pulpmill effluent discharges, turbid mine tailings from Britannia Mine, and gravel washing discharges. The main influence of all these perturbations is on the attenuation of incident radiation in the surface layers of Howe Sound. Of the four, the Squamish River discharge is clearly the overriding factor as seen from the spatial distribution of phytoplankton production and biomass (Fig. 4, 6). When Buchanan and Stockner (1976) simulated productivity in the up-inlet zone of Howe Sound by removing the Squamish River turbidity factor from their model, a marked increase was seen in annual productivity: 235 g $C \cdot m^{-2} \cdot yr^{-1}$ with turbidity, increasing to 339 g $C \cdot m^{-2} \cdot yr^{-1}$ with turbidity removed. The influence of Squamish River turbidity on Stations 1 and 2 is less marked, changing production from 384 to 405 g $C \cdot m^{-2} \cdot yr^{-1}$, by removing the turbidity factor.

The impact of industrial effluents on phytoplankton production in Howe Sound is small in contrast to the influence of the Squamish River, but in bays and subregions of the Sound, these perturbants can influence annual production, reducing it by as much as 25% within affected zones (Stockner and Cliff 1976). Usable marine resources (oysters, clams, seaweeds) within the zones of influence of industrial effluents discharged to Howe Sound are usually impaired, chiefly by wood fibers, sediment, reduced light,

paucity of phytoplankton, or by lethal or sublethal amounts of toxicants (Pedlow 1974, McDaniel 1973, Stockner et al. 1975).

Howe Sound annual production values of 300 and 516 g $C \cdot m^{-2}$ at Station 1 in 1973 and 1974 are similar to the mean of 455 g $C \cdot m^{-2}$ calculated from measurements in Indian Arm (Gilmartin 1964). The averages for all stations in Howe Sound for 1973 and 1974 were considerably lower, 118 and 163 g $C \cdot m^{-2} \cdot yr^{-1}$, and were comparable to the average annual production of 120 g $C \cdot m^{-2}$ for the Strait of Georgia (Parsons et al. 1970). Winter et al. (1975) obtained annual production estimates of 465 g $C \cdot m^{-2}$ for the central basin of Puget Sound, which is similar to our maximum values at Station 1 in Howe Sound. Annual values of the open ocean are considerably less than those seen in Howe Sound, averaging from 30 to 150 g $C \cdot m^{-2} \cdot yr^{-1}$ (Riley 1956, Ryther and Yentsch 1958, Taniguchi 1969).

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Availability of Atmospheric Orthophosphate[1]

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PETERS, R. H. 1977. Availability of atmospheric orthophosphate. J. Fish. Res. Board Can. 34: 918–924.

Phosphorus fractions in 15 samples of rain, rain plus dust, or snow were analyzed to shed light on the role of aeolian P in the nutrient budgets of lakes. Total P levels varied (6.6 to 122.4 μg P/ℓ) but were generally high (mean = 47.0 μg P/ℓ); 76% of this was dissolved. Biologically available orthophosphate comprised an average of 38% of the total. Neither soluble reactive P nor small molecular weight P eluting with ^{32}P-PO_4 in gel filtration were consistently adequate estimates of orthophosphate concentrations.

Key words: nutrient budgets, orthophosphate, phosphorus, bioassay, rain

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Afin de mieux comprendre le rôle du phosphore éolien dans le budget des éléments nutritifs des lacs, nous avons analysé la fraction P dans 15 échantillons de pluie, de pluie avec poussière ou de neige. Les niveaux de P total varient (6.6 à 122.4 μg P/litre), mais sont généralement élevés (moyenne = 47.0 μg P/litre); 76% de ce total sont dissous. L'orthophosphate biologiquement disponible comprend en moyenne 38% du total. Ni le P réactif soluble ni le P de faible poids moléculaire éluant avec le ^{32}P-PO_4 dans la filtration sur gel ne sont des estimés uniformément adéquats des teneurs en orthophosphate.

Received December 21, 1976
Accepted February 22, 1977

Reçu le 21 décembre 1976
Accepté le 22 février 1977

A growing body of evidence suggests that precipitation and dryfall contribute substantial amounts of phosphorus to some pristine and recreational lakes. Schindler and Nighswander (1970) found that rain contributed 40% and snow 20%, of the annual P load of a lake on the Canadian Shield; they did not consider dust. Together snow (Barica and Armstrong 1971) and rain (Armstrong and Schindler 1971) added about 52% (Schindler et al. 1976) to the P inputs of lakes in the Experimental Lakes Area of northwestern Ontario. Dillon (1974) estimated that dryfall and direct precipitation supplied between 0.3 and 79% of the annual P budget of 11 lakes in southern Ontario; higher figures represented lakes with small drainage basins. Rigler (1974) argued that, in general, aeolian P plays an increasingly important role as the surface area of lakes increases relative to the area of their watersheds.

Phosphorus budgets of lakes are based on analyses for total P. However, the importance of a P source lies in the nutritional effect of the supplied P which, in turn, depends on the biological availability of its chemical forms, as well as on the total quantity. Since orthophosphate (PO_4) is readily available to plankton (Einsele 1941; Rigler 1956; Chamberlain 1968), previous authors have estimated biologically available P with the molybdenum blue reaction for soluble reactive phosphate, or SRP (Strickland and Parsons 1968). Schindler and Nighswander (1970) found that 19% of the P in rainwater was SRP. Similar figures (mean = 32, SD = 12, n = 8) were measured in melted snow by Barica and Armstrong (1971), although Schindler and Nighswander (1970) found that only 7% of melted snow was SRP. In some cases (Walton and Lee 1972), SRP does estimate biologically available P; but, Rigler (1966, 1968) and Chamberlain and Shapiro (1969) have shown that SRP frequently overestimates orthophosphate concentrations in lake water. Hence, we cannot assume that SRP measurements adequately reflect the availability of aeolian P for algal utilization.

Gomolka (1975) attempted to estimate the orthophosphate concentration of rainwater using a modification of Rigler's (1966) radiological bioassay, but her methods, though promising, introduced an unacceptably large variation. Lean (1973a, b) and Minear (1972) have shown that

[1]Contribution No. 6 to the Memphremagog project.

Printed in Canada (J4676)
Imprimé au Canada (J4676)

gel filtration of lake water can characterize dissolved compounds according to their molecular weight, but neither author has examined airborne P. This study estimates the orthophosphate concentration of rainwater, rainwater plus dust, and snow, with a modified radiological bioassay and compares these results with SRP determinations and gel-filtration analyses.

Materials and Methods

Sampling

Between July 11, 1975 and July 20, 1976, eight samples of rainwater, six of rainwater plus dustfall, and one of snow were collected at the field station of the McGill Limnology Research Group. The station is about 100 km southeast of Montreal, on the east shore of Lake Memphremagog, Quebec. This is a rural area of woods and pasture. To collect rain plus dryfall, a clean 20-cm funnel was placed in a polyethylene bottle secured to a lake platform about 20 m from shore. The lip of the funnel was about 0.5 m above the lake surface. This sampler was continuously exposed until a rain occurred. When the rain stopped, the sample of dust and rain was collected and frozen until analysis. A similar handling of filtered river water had little effect on the P fractions therein (Peters unpublished data) and it is assumed that rainwater was also unaffected. Samples of rainwater (and entrained "dust") were collected by placing a polyethylene tray (50 × 30 × 10 cm) on the platform at the beginning of a rainstorm and, again, collecting and freezing the sample as soon as the rain stopped. One snow sample was collected from the lake surface on March 6, 1976.

Chemical Analyses

Each sample was analyzed for total phosphorus (TP), soluble phosphorus (SP), and soluble reactive phosphorus (SRP). Two 25-ml subsamples of each whole water sample were placed in 125-ml Ehrlenmeyer flasks for TP analysis. Then, 250 ml of the remaining sample was filtered through a prewashed (Rigler 1964) 47-mm 0.45-μm Millipore membrane filter. Three 25-ml aliquots of the filtrate were placed in Ehrlenmeyer flasks: two for SP and one for SRP analyses. The sample for SRP was then refrozen until analysis.

The TP and SP samples were digested by autoclaving the samples with 2% potassium persulfate (Menzel and Corwin 1965) for 45 min. Then PO_4 concentrations in all samples were analyzed using the molybdenum blue method of Strickland and Parsons (1968).

Gel-Filtration

Gel-filtration analysis separates molecular particles in aqueous solution over a certain range of molecular weights by passing the solution through a column of "cross-linked polydextran gel." Small particles are retarded in the column and elute after large particles.

Pharmacia chromatographic columns with flow adaptors were packed with G-25 Sephadex gel according to methods outlined in the Pharmacia technical bulletins. In 1975 either a 5.0 × 100 cm column or two 2.5 × 50 cm columns joined in series were used. In 1976 all samples were analyzed using two small columns. Columns were calibrated using ^{32}P-PO_4 (New England Nuclear Corporation) and blue dextran to identify the positions of orthophosphate and the void volume (mol wt = ca. 5000), respectively, in the effluent from the columns. These positions bracket the range over which G-25 fine Sephadex provides resolution.

Since Sephadex is only effective on slightly saline solutions, filtrates were made up to 0.3% NaCl; 0.03% of NaN_3 was added to inhibit bacterial growth; and a small amount of ^{32}P-PO_4 was also added to mark the position of PO_4 in each run and to check the recovery of orthophosphate. The columns were then charged with 25 ml of filtrate and flushed with an eluant of 0.3% NaCl and 0.03% NaN_3 in distilled water. Flow rate was maintained at 100 ml/h by a Buchler peristaltic pump.

The effluent from the column was automatically divided into 25-ml fractions by an LKB automatic fractionator. Half-millilitre aliquots of each fraction were dried on planchets and counted using a Nuclear Chicago Geiger-Müller system under gas flow. The remainders of the fractions were digested with $K_2S_2O_8$ and analyzed for P.

Radiological Bioassay

This bioassay begins by measuring the incorporation of ^{32}P-PO_4 by seston following the dilution of lake water with lake-water filtrates containing known amounts of ^{31}P-PO_4 carrier and radiotracer. This generates a set of standard responses against which the effect of an unknown, such as filtered rainwater, can be compared.

Samples of epilimnetic water from the middle of the central basin of Lake Memphremagog (mean TP = 12 μg P/ℓ) were divided into two subsamples one of which was then membrane filtered. The filtrate was divided into 50-ml aliquots to which ^{32}P-PO_4 and carrier were added to raise the filtrate concentrations from 0 up to between 30 and 80 μg P/ℓ, depending on the run. In 1975 as few as 7 standard concentrations were used, but in 1976 this increased to as many as 30, including replications, spaced over 3 days.

Experiments began when 50 ml of unfiltered lake water were mixed with the filtrate samples containing tracer and orthophosphate. After mixture, 5-ml subsamples were withdrawn and filtered on 25-mm 0.45-μm Millipore filters at 2 min and at increasing intervals up to 120 min, in 1976, or, in 1975, 180 min after mixing of filtrate and whole lake water. The filters were immediately glued to planchets, dried, covered with spray varnish, and counted for radioactivity. Half-millilitre replicates of unfiltered water were also counted to determine the total radioactivity.

Filtrates of rainwater, rainwater plus dust, and melted snow were treated similarly. Tracer, but no carrier, was added; the filtrates were mixed with whole lake water; and 5-ml samples were membrane filtered at the same times as during the standard runs. From measurement of the radioactivity of the unfiltered experimental mixture and of the membrane filters, the fraction of the tracer incorporated at the time of each filtration was calculated.

All radiological bioassays were performed during the summer and fall period of rapid orthophosphate turnover (Rigler 1964). Snow and spring rain samples were frozen until then.

Results and Discussion

The results from a typical standard run of the radiological bioassay are plotted in Fig. 1. This shows the amount of tracer incorporated as a function of carrier addition; curves were drawn through values collected at identical times of filtration in different concentrations of ^{31}P-PO_4. The plots show that an increasing fraction of the tracer was accumulated over time at all concentrations and that incorporation decreased as the amount of added PO_4 increased. These results are typical of most lakes, although different graphical presentations are often used (Rigler 1966; Peters 1974). Values from the initial 2-min filtrations were not included in these families of standard curves because the filtration time was too approximate. Variation was also higher in later samples; hence, no values collected after 3 h were used in 1975 and none after 2 h in 1976. Variation in percent incorporation was greatest when ^{31}P-PO_4 additions were small.

Each analysis of filtered precipitation gave seven measurements of the percentage of the tracer incorporated, one at each of the seven filtration times. These were used to make seven estimates of PO_4 concentration, in excess of filtered lake water, by interpolation from the standard curves (Table 1).

Since this technique measures the PO_4 concentration of rainwater above that of filtered lake water, it is essential to add the lake PO_4 concentration to the interpolated values. Lake PO_4 levels are difficult to measure, but Rigler (1966) has provided another radiological bioassay that gives a maximum estimate, possibly an overestimate, of lake water orthophosphate concentrations. His technique requires the rate constants of tracer incorporation by seston in different concentrations of added PO_4. These rate constants can be calculated from data such as that used to construct Fig. 1 and the orthophosphate levels estimated. As expected (Rigler 1966; Levine 1975) the concentration of PO_4 was low in the lake (mean = 0.8 $\mu g/\ell$, SD = ± 0.6, $n = 13$). In two thirds of the precipitation samples, this addition raised the orthophosphate concentration an average of only 3%; the remaining five samples were very low in orthophosphate (mean = 1.54 μg P/ℓ) and the adjustment for lake water represented 40% of this total.

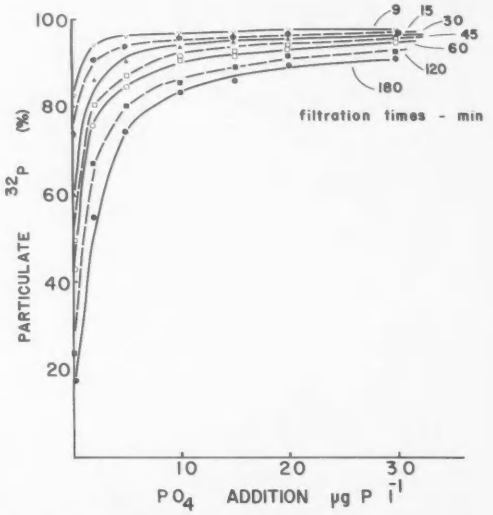

FIG. 1. Family of standard curves used in the modified radiobiological bioassay. These plots relate the response of 1:1 dilutions of whole lake water by filtered lake water to different concentrations of orthophosphate.

Although the radiological bioassay described here depends in part upon Rigler's method, there are several important differences between the techniques. This modification is less precise than Rigler's one-step procedure using whole lake water, because measurements of tracer incorporation by plankton in diluted lake water are more variable and because my estimates depend on two experimentally determined values. Despite those drawbacks, the method used here has several advantages over Rigler's approach. Both techniques involve the calculation of rate constants of ^{32}P-PO_4 incorporation, which is a somewhat arbitrary process (Levine 1975), complicated at times by diphasic kinetics (Lean 1976); but the effects of such problems are reduced in this modification because the older bioassay values provide only a portion of the final estimate of PO_4 concentration. Except for that portion, which may be very small, the new bioassay provides an absolute estimate of PO_4 level and not simply a maximal value. A larger number of samples can be analyzed with the modified techniques, since each estimate requires only one additional uptake

TABLE 1. The estimation of orthophosphate concentration in filtered rainwater collected in August 1975. The amount of tracer incorporated from a 1:1 mixture of ^{32}P-labeled filtrate and whole lake water at each filtration time allows interpolation of the orthophosphate concentration, from a set of standard curves (Fig. 1). Still required is a small correction for the amount of PO_4 in the filtered lake water used to give "0" values of Fig. 1 (see text).

Filtration time (min)	9	15	30	45	60	120	180
Tracer incorporated (%)	93.8	91	83.2	—	77.2	61.9	56.2
Orthophosphate (μg P/ℓ)	.8	1.2	.9	—	1.2	.9	1.1

TABLE 2. Total phosphorus concentration (TP in micrograms per litre), soluble phosphorus (SP, in precent of TP), and orthophosphate concentrations (PO_4 in percent of TP) in precipitation samples. One rain sample (TP = 732 μg P/ℓ; SP = 90%; $PO_4 \gg 60$ μg/ℓ) and the PO_4 value of one rain plus dust sample ($\gg 60$ μg/ℓ) are not included.

	TP (μg P/ℓ)	SP (%)	PO_4 (%)
Rain			
$\bar{x} \pm$ SD	39.6±23.8	88±11	48±38
range (n)	13.5–78 (7)	71–90 (6)	1–100 (7)
Rain + dust			
$\bar{x} \pm$ SD	51.4±49	64±17	25.7
range (n)	6.6–122.4 (5)	45–83 (5)	4.4–56 (3)
Snow			
$n = 1$	77.8	53	7.8

experiment; Rigler's technique requires a series of runs at several levels of added phosphate for each unknown. This bioassay also permits the analysis of samples without active planktonic uptake, such as rainwater, river water and stored samples of filtrate; this is not possible using the original method. A minor disadvantage, that the unknown sample must have a higher PO_4 concentration than the zero level in the calibration series, could be offset by adding a small amount of carrier (ca. 1 μg PO_4-P/ℓ) to the unknowns before analysis.

Both assays are conceptually similar: they estimate PO_4 concentration from changes in the short-term incorporation of ^{32}P-PO_4 following manipulation of the plankton's orthophosphate environment. Rapid tracer uptake in lake water (Rigler 1964; Peters 1975, 1976) and low limnetic PO_4 levels give the methods great sensitivity. Since this uptake is primarily biological (Rigler 1956; Pomeroy 1960; Lean and Rigler 1973; Paerl and Lean 1976), both bioassays are measures of orthophosphate from the "point of view" of the plankton and hence of biologically available P. Neither technique can deal with the larger question of the availability of soluble organic or particulate P.

Table 2 shows the results of chemical analysis for total and soluble P and the radiobiological assays for PO_4. Although there was considerable variation between samples, most of the P in precipitation was dissolved and a substantial fraction was in a biologically available form, PO_4. The different types of precipitation were not significantly different in their P fractions; however, the average values of rain and of rain plus dust suggest differences that might be verified by paired samples of the two.

Figure 2 shows that SRP frequently exceeded the PO_4 concentration. Two, not necessarily exclusive, explanations have been proposed for this difference in lake water. Rigler (1966, 1968) suggested that labile organic phosphate complexes are destroyed by the acid molybdate reagents. Chamberlain and Shapiro (1969) suggest arsenate interference as well, since high levels of arsenate, which analyzes as PO_4, can be found in lake water. The results of gel-filtration analysis suggest that in rainwater, arsenate or small molecular weight organic P is more likely the source of interference.

Figure 3 plots the distribution of P in the effluent from gel filtration in two typical runs. Both distributions suggest that the bulk (80%) of the recovered P eluted with ^{32}P-PO_4 and thus had a molecular weight similar to orthophosphate. Very little P occurred in other fractions. Similar results were obtained in all analyses (Table 3).

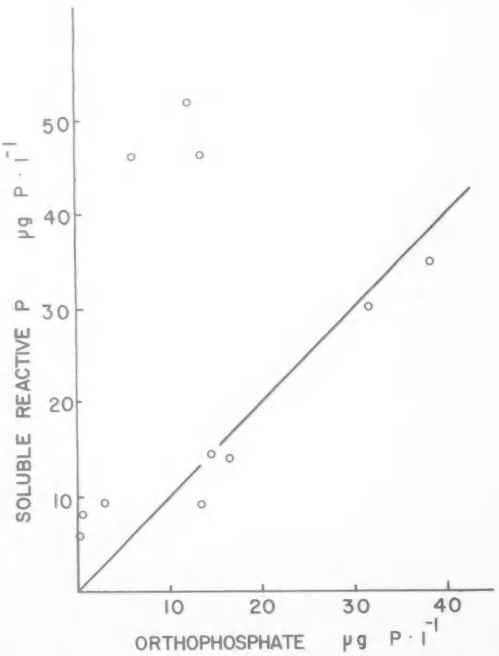

FIG. 2. The relationship of biologically available P, as determined by the radiological bioassay for orthophosphate, and soluble reactive phosphate.

The percent recoveries of tracer and tracee were similar to those reported by Peters and Lean (1973) and Minear (1972).

In the run represented by the upper panel of Fig. 3 the concentrations of PO_4, SRP, and small molecular weight P (SMWP) agreed well. In that of the lower panel, however, PO_4 was much less than SRP or SMWP. Similar discrepancies occurred in other runs; in all but a few cases SMWP overestimated PO_4 (Fig. 4A). A far better correlation exists between SRP and SMWP (Fig. 4B).

These results show that whatever interferes in chemical analysis for PO_4 has a molecular weight similar to PO_4. This precludes most organic phosphates, especially large molecular weight colloids (Lean 1973a, b), which seem likely sources of acid-labile phosphorus. Arsenate, which has a molecular weight only slightly greater than PO_4, may seem a more probable choice. If arsenate is the source of interference in these analyses, the data of Table 2 must be based on overestimates. Consequently, a correction factor was calculated as the average by which SRP and SMWP exceeded the PO_4 values. This value was subtracted from the measured TP and SP to give the "minimal" estimates presented in Table 4. The trends are not changed even though the total values are lowered. However, there is no obvious, local source of arsenate in the Lake Memphremagog area. Since simultaneous arsenate analyses were, unfortunately, not performed, the possibility that high SRP and SMWP values reflect the presence of small, labile organic phosphates cannot be excluded, for these molecules could also elute with ^{32}P-PO_4 in gel filtration.

Accepting the figures in Table 2, with the caveat that arsenate interference may occur, I conclude that these rain samples contained substantial amounts of phosphorus; a large proportion (76%) of this was dissolved and at least half of this dissolved P was biologically available.

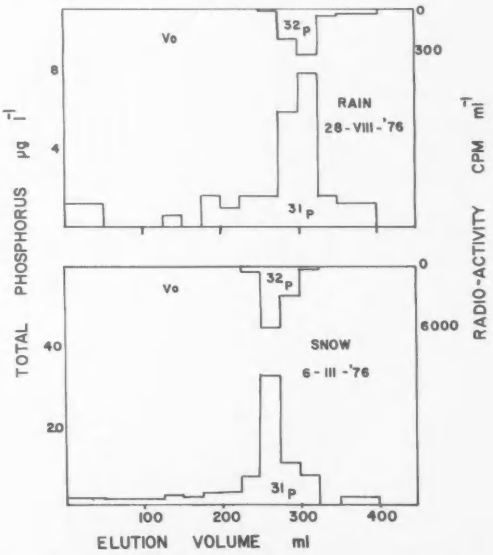

FIG. 3. Elution profiles of ^{32}P-PO_4-labeled rainwater (*upper*) and melted snow (*lower*) produced by passing the samples through gel filtration and collecting successive 25-ml fractions of effluent. V_0 indicates the void volume in each run.

TABLE 3. The percentage of recovered P that elutes at void volume (V_0) and with ^{32}P-PO_4 as small molecular weight P (SMWP) in all gel-filtration analyses of precipitation samples. The recoveries of tracer and total dissolved P are also indicated.

		Recovery (%)	
V_0	^{32}P-PO_4	^{32}P-PO_4	P
12±12	78±18	82±17 (n = 11)	88±24 (n = 15)

TABLE 4. Minimum estimates of TP, SP, and PO_4 levels in precipitation calculated by assuming that arsenate interference caused overestimates in Table 2; SP and PO_4 are expressed as percent of TP.

	TP (μg P/ℓ)	SP (%)	PO_4 (%)
Rain			
mean ± SD	31.3 ± 15	75 ± 23	51.3 ± 36
range (n)	13.5–51.0 (6)	35–100 (6)	1.3–100 (7)
Rain + dust			
mean ± SD	23.6 ± 21	56 ± 11	36.6 ± 18.6
range (n)	4.6–46.5 (4)	45–77 (4)	8.6–56 (5)
Snow			
$n = 1$	25.1	24	24

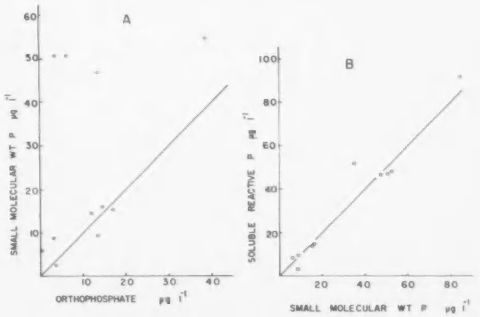

FIG. 4. A, The relationship between orthophosphate concentration and the small molecular weight phosphorus that elutes with ^{32}P-PO_4 in gel-filtration analysis; B, the relationship between soluble reactive phosphorus and small molecular weight phosphorus. One high value (SRP = 544, SMWP = 605) is not plotted.

If these amounts are at all representative, rainfall can contribute substantial amounts of utilizable P to the plankton of lakes.

Acknowledgments

I thank S. Angelides, W. Kulakowski, R. Leon, K. Webster, and D. Wong for their help in technical aspects of this study. Funds are provided to the Memphremagog project by the National Research Council of Canada, the Inland Waters Directorate of Environment Canada, and the Ministry of Education of the Province of Quebec. Funds for the purchase of gel-filtration equipment were provided by a grant from the Faculty of Graduate Studies and Research, McGill University. Each of these agencies is gratefully acknowledged.

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Reconstruction of Yellow Perch (*Perca flavescens*) Cohorts from Examination of Walleye (*Stizostedion vitreum vitreum*) Stomachs[1]

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FORNEY, J. L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. J. Fish. Res. Board Can. 34: 925–932.

Number of young perch (*Perca flavescens*) consumed by walleye (*Stizostedion vitreum vitreum*) in Oneida Lake was determined from analysis of feeding chronology and digestion rates. Young perch were ingested between sunset and sunrise and digestion rates were estimated from the decrease in weight of perch in stomachs during the day. Walleye predation began in late June and by October the number of young consumed ranged from 17,940 to 242,900·ha^{-1} in 1971–73. Concurrent studies indicated an additional 590 to 56,130 young were eaten by adult perch.

Minimum population of young perch in June was calculated by adding to the number of young that survived to fall, the number consumed by walleye and adult perch. Populations reconstructed in this manner approximated independent estimates of the pelagic population in June. Mortality of young perch was apparently attributable to predation by percids and reconstructed populations accurately portrayed seasonal trends in abundance of young perch.

Key words: predation, walleye, yellow perch, digestion, mortality

FORNEY, J. L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. J. Fish Res. Board Can. 34: 925–932.

L'analyse de la chronologie des repas et des vitesses de digestion ont servi à déterminer le nombre de jeunes perchaudes (*Perca flavescens*) consommées par le doré jaune (*Stizostedion vitreum vitreum*) dans le lac Oneida. Les jeunes perchaudes furent absorbées entre le coucher et le lever du soleil, et les vitesses de digestion ont été estimées à partir de la diminution de poids des perchaudes dans les estomacs au cours de la journée. La prédation par les dorés jaunes en 1971–73 commença vers la fin de juin et, en octobre, le nombre de jeunes consommés variait de 17 940 à 242 900·ha^{-1}. Des études simultanées indiquent que 590 à 56 130 jeunes de plus sont mangés par des perchaudes adultes.

La population minimale de jeunes perchaudes en juin a été calculée en ajoutant au nombre de jeunes survivant jusqu'en automne le nombre consommé par les dorés jaunes et les perchaudes adultes. La taille des populations calculée de cette manière se rapproche d'estimations indépendantes de la population pélagique en juin. La mortalité des jeunes perchaudes est apparemment attribuable à la prédation par les percidés, et les populations ainsi reconstruites donnent une image exacte des tendances saisonnières dans l'abondance des jeunes perchaudes.

Received November 16, 1976
Accepted February 18, 1977

Reçu le 16 novembre 1976
Accepté le 18 février 1977

YOUNG yellow perch (*Perca flavescens*) in Oneida Lake, New York, are the principal prey of walleye (*Stizostedion vitreum vitreum*) (Forney 1974) and significant numbers of young perch are also consumed by adult perch (Tarby 1974). Walleye and yellow perch constituted about 85% of the catch in experimental gill nets in 1960–73 and these two species were nearly as well represented in trawl and trap net catches during the same period. The predominance of walleye and older perch and the importance of young perch in their diet suggested these two species might consume a significant proportion of a perch cohort.

Few studies have examined the pattern of mortality and changes in abundance of young fish during the 1st yr of life. If predation is the primary cause of mortality, a minimum estimate of the initial size of a cohort could be generated by summing over a season the number of young consumed by the predator population. A cohort reconstructed in this manner would be analogous to a "virtual population" derived by summing

[1]Contribution from Federal Aid in Fish Restoration Project F-17-R New York.

Printed in Canada (J4643)
Imprimé au Canada (J4643)

the catch from a year-class over its life span in a fishery (Fry 1949).

Feasibility of reconstructing cohorts of yellow perch from examination of predator stomachs was evaluated in 1971–73. This paper outlines the method of estimating numbers of perch consumed by walleye. Concurrent studies provided data on cannibalism by adult perch. Combined consumption was summed over the period June to October to determine the minimum size of cohorts produced in 1971–73. How accurately reconstructed populations portrayed seasonal trends in abundance of young perch was evaluated from catches in high-speed Miller samplers (Noble 1968) in June and trawls in late summer.

Oneida is a moderately eutrophic lake with a surface area of 20,700 ha and a maximum depth of 16.8 m (Greeson 1971). Adult walleye and yellow perch are widely distributed and occupy littoral and limnetic areas. Yellow perch usually spawn in late April and eggs hatch in May. Parental stock is fairly stable but variation in climatic conditions during egg incubation induces wide fluctuations in larval abundance (Clady 1976). Some young perch appear in the littoral zone in June, but others remain pelagic into July (Lin 1975). Walleye begin feeding on young perch when the cohort attains a mean length of about 18 mm in June and predation continues after young are demersal.

Materials and Methods

Daily consumption of age 0 yellow perch by walleye was estimated from the number of young observed in stomachs and the rate of gastric digestion. Walleye were captured in otter trawls fished at depths of 5–12 m within a 4-km radius of Shackelton Point. Age III and IV walleye were predominant in the catch in 1971, I and IV in 1972, and II and V in 1973. Samples were collected at 4–5-h intervals from sunrise to sunset each week from June through September 1971–73 and occasionally trawling was continued through a 24-h period. Walleye stomachs were examined by inserting an open glass tube. The food bolus was removed and the tube reinserted to visually check the stomach for any remaining food. Regurgitation of stomach contents during capture was not considered a significant source of error, since partly digested fish were never observed in the cod ends of trawls.

Undigested remains of fish in stomachs were weighed, enumerated, and identified to species when possible. About half of the fish in stomachs of walleye collected at sunrise in June were identifiable to species and the proportion increased to over 90% by late summer. Unidentified remains were assigned to species based on the species composition of the identifiable portion. Samples of intact age 0 perch were measured and initial weight of perch ingested predicted from a length–weight regression. Walleye captured during each sampling period were pooled and meal size expressed as number or weight of perch per kilogram of walleye.

Digestion rate was estimated from the decrease in stomach contents during the day. It will be shown later that nearly all prey were consumed between sunset and sunrise. Thus, the quantity of food in stomachs at sunrise could be considered the initial meal size and the rate of depletion estimated from subsequent samples taken during the day. The field method emulates an aquarium experiment in which a quantity of food is fed to a group of fish and subsamples killed at intervals to determine the amount of food remaining in stomachs.

Daily ration of age 0 perch per kilogram walleye was multiplied by the biomass of age I and older walleye to determine the number of perch consumed by the walleye population. Number of age IV and older walleye in April 1970, 1972, and 1974 was estimated by mark and recapture following procedures developed in earlier years (Forney 1967). Numbers during intervening periods were approximated from the distribution of mortality between successive biannual population estimates. Annual natural mortality was about 0.05 (Forney 1967) and the seasonal distribution of walleye tag returns from anglers was used to apportion fishing mortality between successive population estimates. Minimum numbers of walleye in age-groups I–III were known from the contribution of individual year-classes to the population at age IV. It was assumed age-groups I–III experienced the same natural mortality as older walleye, but age III walleye experience half the fishing mortality and I and II were not vulnerable to angling. Seasonal growth in weight was determined from samples taken during the spawning run and in trawls and gill nets during the summer. Products of observed weights and numbers in each age-group were summed to determine population biomass at monthly intervals.

Abundance of young perch was estimated in early June from the catch in Miller samplers at 42 sites. A stratified random sampling design with proportion allocation of effort was followed as outlined by Noble (1968). At each site four samplers spaced at intervals to a maximum depth of 5.5 m were towed simultaneously at a speed of 13 $km \cdot h^{-1}$. Volume strained was determined and catch per cubic metre was weighted by the volume of each strata to estimate mean density of perch. Young perch are capable of avoiding samplers, and avoidance factors were developed by comparing the catch in standard samplers with modifications of the gear and sampling technique that resulted in higher catches (Noble 1970). Because perch may avoid even the most efficient gear tested, avoidance factors may be underestimated and consequently estimates of perch density are probably conservative.

Abundance of young perch in late summer was estimated from the catch in trawls fished at 17 sites at weekly intervals. The lake was stratified along depth contours and catches at depths of 2.5-12 m were weighted by the area of the strata. The relation between the natural logarithms of mean weekly catches and dates of capture were defined by least

squares regression. Abundance of cohorts was predicted from the fitted regressions. Trawling speed was 3.4 km·h^{-1} and a standard 5-min haul swept about 1000 m^2 based on the width of the net under tow.

Results

Feeding Chronology

Weight of food in stomachs of walleye collected at about 4-h intervals in 1971 showed a fairly consistent decline during the day (Fig. 1). Walleye fed almost exclusively on fish in 1971 and over 98% of the fish identified were young yellow perch. Freshly consumed fish with skin intact were common in stomachs of walleye caught at 0530 but were observed in < 2% of the stomachs of walleye taken at 0930, 1330, or 1700 and only in age I and II walleye. This suggests that most perch were eaten at night and the decrease in weight of fish in stomachs during the day is an estimate of the stomach evacuation rate.

Stomachs were evacuated rapidly in June and July and most stomachs were empty by late afternoon (Fig. 1). In August and September the decrease in weight of food in stomachs was slower and remains of prey were still present in stomachs at 1700. Increase in size of perch from 0.24 g on June 30 to 2.08 g on September 24 is the most likely explanation for the increase in stomach evacuation time, since water temperature remained within a 19–23°C range throughout the summer. High surface to volume ratio of small perch would favor rapid evacuation if rate of digestion is a function of surface area exposed to enzyme activity as suggested by Tyler (1970).

The diurnal decrease in weight of food in stomachs of walleye captured in 1972 and 1973 was well defined in July when age 0 perch were the primary prey (Fig. 2). But in late summer diet was more diverse and included yearling perch, age 0 white perch (*Morone americana*), and pumpkinseed (*Lepomis gibbosus*). Heterogeneity in size of prey resulted in a less consistent reduction in weight of food in stomachs during the day. However, there was a clearly defined diurnal decrease in number of fish in stomachs which would be anticipated if most prey were ingested at night (Forney 1973).

Continuation sampling through the night provided limited data on the pattern of nocturnal feeding in July 1972–73. On most nights there was a progressive increase in weight of fish in walleye stomachs between sunset and sunrise (Fig. 2). Feeding apparently began soon after sunset, since walleye netted an hour after sunset often contained freshly consumed fish some of which were still alive when removed from stomachs. The increase in number and weight of prey and stage of digestion of fish in stomachs taken at 2–3-h intervals suggested feeding was continuous at night. However, feeding rates of walleye captured in bottom trawls may not accurately portray the nocturnal feeding pattern of the population. Walleye catches were usually lower at night than during the day, which suggests that some fish were off bottom or moved into areas where trawling was not conducted.

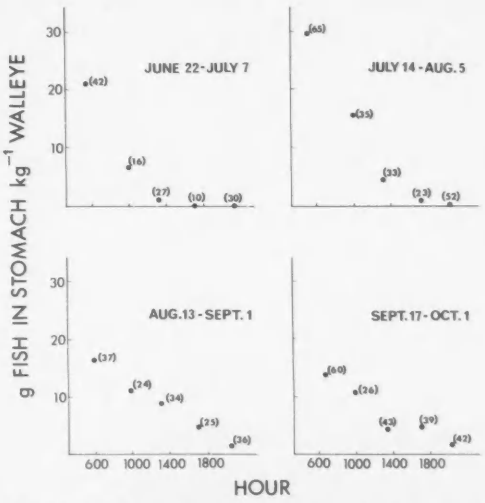

Fig. 1. Weight of fish in stomachs of age I and older walleye (*Stizostedion vitreum vitreum*) collected by trawling at about 4-h intervals during the day in 1971. Samples taken on several days during periods of the summer were combined. Number of fish examined is shown in parentheses.

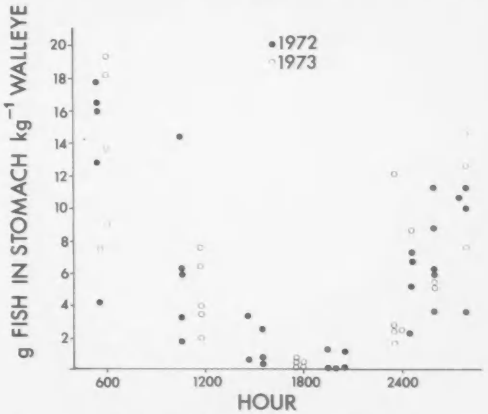

Fig. 2. Weight of fish in stomachs of walleye collected at intervals during 24-h periods between July 3 and August 3, 1972–73. Each point based on catch of 10 or more walleye in trawls.

Evacuation Rate

Rate of evacuation was determined from samples collected on 34 days in 1971–73 when age 0 perch comprised over 90% of the identifiable food items in stomachs of walleyes. Linear regressions were fitted to the natural log of the weight of prey fish in stomachs (grams of prey per kilogram walleye) against time with time zero when the first sample was taken after sunrise. Thus, the model assumed is

$$W = W_0 e^{-bt}$$

where W is the weight remaining in the stomach, W_0 the initial weight of a meal, b the regression coefficient, or instantaneous rate of food depletion, and t the elapsed time in hours. Regressions were based on three to five samples taken between 0530 and 2030 except for 2 days in June when all stomachs examined after the first two sampling periods were empty.

Rates of food depletion were generally high in early summer when age 0 perch averaged < 0.3 g and coefficients decreased during the season as the mean weight of perch increased to 2–7 g by fall. Weight of food in stomachs of walleye at sunrise and water temperature did not appear closely related to food depletion rates. Relative importance of prey weight, meal size, and temperature as factors influencing evacuation rate was examined by fitting a polynomial regression with evacuation rate as the dependent variable to samples taken on 35 days when age 0 perch were the predominate prey. Of the variables examined, only prey weight accounted for a significant proportion of the variability in digestion rate. Evacuation rates estimated from the diurnal decrease in weight of food in stomachs may have lacked sufficient precision to detect effects of meal size and temperature, or the range in these variables was too narrow to demonstrate their effect. Quantity of food in stomachs varied from 0.3 to 3.3% of body weight, and temperatures fell within a relatively narrow range of 17–23°C. Swenson and Smith (1973) found that large meals and low temperatures suppressed digestion rates of walleye held in raceways.

The decrease in evacuation rate during the summer may be explained by changes in the surface–weight ratio as mean size of perch increased. Disintegration of particles during digestion may occur only at the surface. The surface area of an ellipsoidal-shaped fish should increase as the square of the dimensions, and dimensions are a cubic function of the weight. Thus, digestion rate should be proportional to the two-thirds power of the weight (Tyler 1970). The concept of surface dependent digestion offers theoretical justification for relating evacuation rate to the cube root of prey weight (Fig. 3). The following second degree polynomial adequately fit to the data:

$$b = -.6590 + .5554\, X^{\frac{1}{3}} - .1474\, X^{\frac{2}{3}}$$

where b is the instantaneous rate of food depletion and X the prey weight. Analysis of variance confirmed deviations from linearity were significant ($P < 0.05$).

Evacuation rates calculated from the curve appear reasonably compatible with results of laboratory studies. Swenson and Smith (1973) fed walleye fathead minnows (*Pimephales promelas*) that weighed 0.8, 1.1–1.9, and 3.1–5.0 g. Times required to digest 90–97% of a meal was 12 h for minnows weighing 0.8 g and increased to 16 and 24 h for larger size-classes. Time required to digest yellow perch of corresponding sizes can be estimated by substituting into the evacuation rate model values for b from Fig. 3. The weight of food remaining in the stomach was assigned a value of 0.05 W_0. Original weight of the meal (W_0) was selected and the equation solved for t. Estimated 95% evacuation times for perch weighing 0.8, 1.5, and 4.0 g are 11, 14, and 20 h, respectively. Lake temperatures averaged 21°C compared to temperatures of 20°C for 0.8-g minnows and 14.5°C for laboratory tests with larger minnows (Swenson and Smith 1973). Higher lake temperatures may explain the slightly shorter evacuation times for unconfined walleye in this study.

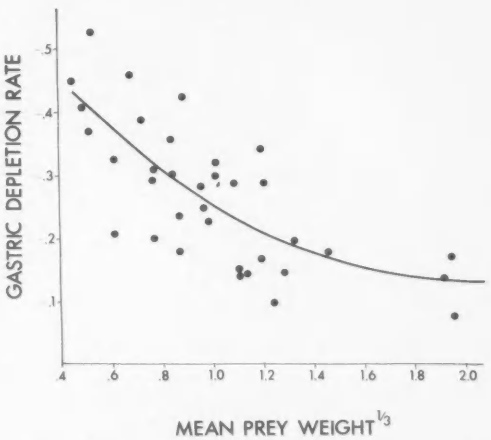

FIG. 3. Mean weight of age 0 yellow perch (*Perca flavescens*) ingested by walleye on days in 1971–73 and gastric digestion rate estimated from decline in weight of fish in stomachs of walleye captured at intervals during daylight hours.

TABLE 1. Daily consumption of age 0 yellow perch (*Perca flavescens*) per kilogram walleye (*Stizostedion vitreum vitreum*) estimated at weekly intervals beginning June 13, 1971, June 4, 1972, and June 18, 1973.

	1971		1972		1973	
Wk	Stomachs examined at sunrise	Daily meal perch·kg^{-1}	Stomachs examined at sunrise	Daily meal perch·kg^{-1}	Stomachs examined at sunrise	Daily meal perch·kg^{-1}
1	18	350	29	48	14	31
2	11	239	9	53	40	87
3	8	248	16	110	64	49
4	23	145	24	99	29	21
5	16	92	16	35	19	20
6	26	69	12	26	27	11
7	10	83	31	42	35	11
8	13	73	28	15	19	5
9	8	10	20	4	23	5
10	6	24	22	3	25	3
11	12	32	17	5	35	1
12	21	28	31	2	40	4
13	—	—	15	4	32	3
14	26	13	14	0	28	1
15	11	19	17	1	47	2
16	23	7	—	—	37	1
17	—	—	25	1	63	1
18	—	—	—	—	11	1
19	—	—	—	—	87	1

CONSUMPTION OF YELLOW PERCH

Number of fish remains in stomachs of walleye at sunrise represents the daily meal if gastric evacuation times are greater than the duration of the sunset–sunrise feeding period but less than 24 h. When perch were large and evacuation times exceeded 24 h, inclusion of fish ingested during earlier feeding periods was avoided by ignoring particles less than a predetermined weight. Because young perch were uniform in size and few larger fish were ingested, gaps in size distribution of particles in stomachs were usually obvious. Conversely, small perch ingested at the beginning of a feeding period may be passed from the stomach before sunrise. On days when estimated evacuation times were shorter than the nocturnal feeding period the number of fish observed in stomachs was multiplied by the number of hours in the nocturnal feeding period and divided by the evacuation time. This adjustment is based on the assumption nocturnal feeding is continuous, which has not been adequately documented, but any errors introduced are probably minor unless feeding activity is strongly skewed.

Number of perch consumed per day per kilogram walleye in 1971 declined from 350 in June to 6 in October (Table 1). The seasonal decline in consumption was equally pronounced in other years but number of perch ingested was much lower. The decrease in perch consumption during the summer was apparent in all age-groups of walleye and was not unique to the area near Shackelton Point. Walleye taken at two additional locations in 1973 ingested about the same number of perch per day during the season as those caught near Shackelton Point. Reduced consumption of perch suggests a rapid decline in abundance or availability of perch because weight of food in stomachs during late summer in 1972–73 seldom exceeded 2% of body weight compared to 4–6% in 1971.

RECONSTRUCTION OF PERCH COHORTS

Cohorts of young perch were reconstructed by adding to the number remaining in October, the number eaten by walleye and adult perch in preceding weeks (Fig. 4). Density of perch on selected dates in October was calculated from regressions fitted to the catch per hectare swept by trawls in late summer and fall. Number of perch consumed was the product of the daily ration expressed as perch per kilogram walleye and the biomass of walleye. Between mid-June and October walleye consumed 242,900 perch·ha^{-1} in 1971, 80,730 in 1972, and 17,940 in 1973. During the same period predation by adult perch accounted for an additional 56,130 young·ha^{-1}

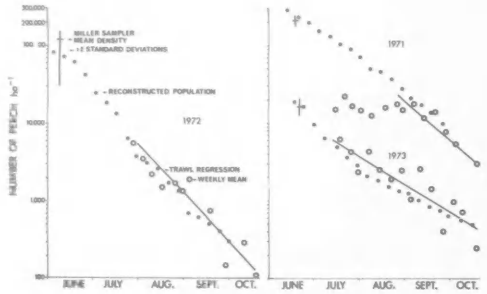

FIG. 4. Density of age 0 yellow perch reconstructed from number consumed by walleye and older perch (●). Catch in Miller samplers in June and trawl catch per area swept in August–October (○) are independent estimates of density.

in 1971 but only 4200 in 1972 and 590 in 1973 (Tarby 1975).

The number of perch consumed by walleye and adult perch when added to the number remaining in October approached or exceeded the number in early June estimated from the catch in Miller samplers.

	No·ha^{-1}	
	Reconstructed	Miller sampler
June 18, 1971	240,000	216,000
June 8, 1972	79,000	121,000
June 21, 1973	17,000	17,000

This implies that predation by walleye and cannibalism by perch accounted for most of the loss of young perch between June and October. The decrease in numbers of perch, as portrayed by reconstructed populations in 1971–73, suggests a fairly constant exponential rate of mortality during the summer (Fig. 4). The same mortality pattern is evident in examining trawl catches.

Catches of young perch in trawls followed closely the decline in the reconstructed population in 1972 and 1973 (Fig. 4). Slopes of regressions fitted to natural logarithms of trawl catches from July to October were 0.043 and 0.027, suggesting the daily mortality rate in 1972 was twice that in 1973. Over the same period reconstructed populations decreased at an average rate of 4.3%·day^{-1} in 1972 and 2.0%·day^{-1} in 1973. Reconstructed populations and trawl catches would be expected to show a parallel decline if most mortality during late summer was attributable to predation by percids.

Samples taken in midwater and bottom trawls indicated transition of perch from the pelagic to demersal mode occurred in late July 1972 and early June 1973 (Lin 1975). Failure of trawl catches to follow the same trend as the reconstructed population in 1971 suggests part of the perch population may have remained pelagic into August. Gradual recruitment of pelagic perch to the demersal population would explain the failure of trawl catches to show a decline in August. Although vertical distribution was not monitored in 1971, growth of perch was exceptionally slow (Noble 1975) and small size may have delayed transition.

Discussion

Measurement of stomach evacuation rate provides a direct approach for estimation of food consumption when combined with information on quantity of food in stomachs (Davis and Warren 1968). Digestion rates have generally been measured in the laboratory and extrapolated to the field. However, in this study walleye ingested perch during a relatively short 8–10-h nocturnal feeding period and evacuation rates could be derived from the decrease in weight of perch in stomachs of walleye collected at intervals during the day. Evacuation rates of unconfined walleye in Oneida Lake and walleye acclimated in raceways to accept meals voluntarily (Swenson and Smith 1973) were similar, which suggests confinement has little effect on rate of gastric evacuation.

Evacuation of stomachs occurred during the day and feeding did not resume until after sunset, although walleye stomachs in June and July were often empty by early afternoon. Comparison of feeding chronology of walleyes captured in bottom trawls and canned gill nets set 2–3 m below the surface in July–August 1971 did not reveal any differences (unpublished data). Although young perch were pelagic, none of the 109 walleye caught in gill nets set for 3–4-h intervals during the day contained recently ingested fish and the quantity and stage of digestion of fish in stomachs was similar to that anticipated from analysis of trawl caught fish.

Evidence that the number of age 0 perch consumed by walleye and adult perch approximately matched the number of young available in June is not surprising. Walleye in Oneida Lake feed mostly on age 0 perch and annual growth and recruitment of walleye fluctuate in response to variation in abundance of young perch (Forney 1965, 1976). This suggests intense competition for prey and the minor contribution of yearling perch to the diet of walleye is evidence that few perch survive to age I (Forney 1974). Although centrarchid bass and esocids also utilize young perch, their impact on perch cohorts appears insignificant in Oneida Lake.

Walleye predation began in June when perch

were pelagic and weighed < 0.1 g. The daily ration in June was several hundred perch per kilogram walleye and over two thirds of the perch available in early June were consumed before cohorts became demersal in 1971–73. Walleye predation on pelagic perch sharply reduces the number available to predators that show a lesser proclivity to invade the limnetic zone. Thus, inclusion of age 0 perch consumed by centrarchid bass and esocids would probably not significantly inflate reconstructed population estimates based solely on consumption by walleye and adult perch.

The most striking feature of predation in this demographically simple association is the rapid, continuous depletion of age 0 perch over a wide range of densities. Neither the shift in vertical distribution of perch during the summer nor their increase in size produced a marked change in rate of predation. Populations reconstructed from estimates of numbers of perch consumed showed a steady decline from June to October, which suggests a fairly constant rate of mortality (Fig. 4). Predation continued unabated as density declined below $1000 \cdot ha^{-1}$ in 1972 and 1973. Although the number of alternative prey in the diet of walleye increased in late summer (Forney 1974), there was no evidence that increased utilization of other prey reduced mortality of age 0 perch. By May when perch were age I, trawl catches indicated densities of 110, 3, and $100 \cdot ha^{-1}$ in 1972, 1973, and 1974, respectively. Proportion of the overwinter loss attributable to walleye predation is unknown, but the continued depletion of the 1971–73 cohorts suggests low density does not afford much protection from predation.

Rapid depletion of perch year-class by walleye is probably not unique to Oneida Lake. Walleye in many waters grow at rates well below their physiological maximum, which suggests that prey density is often low. Predation on small pelagic perch is not an optimal feeding strategy in a system where food is limited. A prudent population of walleye could have nearly doubled perch production in 1972 by delaying predation for 2 wk. The value of abstinence can be demonstrated by plotting weekly estimates of perch density (Fig. 4) against mean weight of perch on corresponding dates in the manner described by Allen (1951). The area under the curve shows that production would increase from 27 kg perch$\cdot ha^{-1}$ between June 7 and September 15 to 49 kg$\cdot ha^{-1}$ if the onset of walleye predation was delayed until June 21. Efficiency of the walleye as pelagic predator reduces forage production but this strategy also denies other predators food, which should minimize the risk of extirpation through competition.

Earlier studies in Oneida Lake showed that numerically abundant year-classes of perch generally experienced lower mortality during late summer of their 1st yr than small year-classes (Forney 1971). It was hypothesized that walleye predation generated differences in mortality and predation was more intense in years when perch density was low. Comparison of number of young perch available and number consumed in 1971–73 leaves little doubt that loss of perch is largely attributable to walleye predation. Perch mortality was relatively low in 1971 when perch were abundant and high in 1972 when perch were scarce, which supports the assumption that hunger increases the rate of predation. Although survival of the 1973 year-class was high despite low perch density (Fig. 4), this may be explained by the drop in walleye biomass from 25 to 10 kg$\cdot ha^{-1}$ between 1972 and 1973. If it is postulated that rate of attack is proportional to predator biomass, mortality rate in 1973 should be increased by a factor of 2.5 for comparison with 1972. Daily instantaneous mortality coefficients estimated from trawl catches shown in Fig. 4 were 0.043 in 1972 and 0.027 in 1973. Thus, the predicted rate of mortality in 1973 would be 0.0682, which is higher than the observed rate in 1972 and consistent with the concept that rate of predation is hunger dependent.

Hunger is only one of several factors that have been shown to play a prominent role in establishing rate of predation in controlled experiments (Ware 1972). Evaluation of other factors in natural systems is a necessary step in the development of a general model of predation. In waters where a few predators consume most of the prey, reconstruction of prey populations from examination of predator stomachs can provide data for testing predator–prey parameters free from the physical constraints of the aquarium.

Acknowledgments

Thanks are due D. S. Robson, R. L. Noble, M. D. Clady, and M. J. Tarby for their counsel, comments, and assistance during various phases of this study. Illustrations were prepared by A. A. Klock.

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Susceptibility of Salmonid Species and Hatchery Strains of Chinook Salmon (*Oncorhynchus tshawytscha*) to Infections by *Ceratomyxa shasta*[1]

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ZINN, J. L., K. A. JOHNSON, J. E. SANDERS, AND J. L. FRYER. 1977. Susceptibility of salmonid species and hatchery strains of chinook salmon (*Oncorhynchus tshawytscha*) to infections by *Ceratomyxa shasta*. J. Fish. Res. Board Can. 34: 933–936.

Nine salmonid species and nine hatchery strains of chinook salmon (*Oncorhynchus tshawytscha*) were examined for susceptibility to infection by *Ceratomyxa shasta*. All salmonid species tested were susceptible to infection by this myxosporidan, although no deaths occurred in the Atlantic salmon (*Salmo salar*). The level of resistance varied widely among the different species. A low prevalence of ceratomyxosis occurred in hatchery strains of chinook salmon from the Columbia River basin, while those chinook strains derived from outside this drainage system were highly susceptible to the parasite.

Key words: *Oncorhynchus tshawytscha*, salmonidae, ceratomyxosis, *Ceratomyxa shasta*, resistance, susceptibility

ZINN, J. L., K. A. JOHNSON, J. E. SANDERS, AND J. L. FRYER. 1977. Susceptibility of salmonid species and hatchery strains of chinook salmon (*Oncorhynchus tshawytscha*) to infections by *Ceratomyxa shasta*. J. Fish. Res. Board Can. 34: 933–936.

Nous avons étudié la susceptibilité à l'infection par *Ceratomyxa shasta* de neuf espèces de salmonidés et de neuf lignées de pisciculture de saumons chinook (*Oncorhynchus tshawytscha*). Toutes les espèces de salmonidés testées sont susceptibles à l'infection par cette myxosporidie, bien qu'il ne se produise aucune mortalité chez le saumon atlantique (*Salmo salar*). Le niveau de résistance varie largement entre les différentes espèces. On trouve une faible prévalence de cératomyxose dans des lignées de pisciculture de saumons chinook du bassin du fleuve Columbia, alors que les lignées de saumons chinook provenant de l'extérieur de ce réseau sont fortement susceptibles au parasite.

Received December 10, 1976
Accepted March 8, 1977

Reçu le 10 décembre 1976
Accepté le 8 mars 1977

SALMONIDS infected with *Ceratomyxa shasta* have been found in Canada (Margolis and Evelyn 1975) and Idaho, but the infectious stage is believed to be limited to portions of Washington, Oregon, and northern California (Schafer 1968; Sanders et al. 1970). Chemotherapeutic agents effective against this parasite have not been developed (Leith and Moore 1967; Sanders et al. 1972; Wood 1974; Udey et al. 1975). However, Schafer (1968) and Sanders et al. (1970) noted differences in susceptibility among salmonid species and the level of resistance among hatchery strains of the same salmonid species. In the present study these variations in susceptibility were examined to develop possible management practices for the stocking of waters containing the infectious stage of *C. shasta*.

Materials and Methods

All fish selected for this study had no history of prior exposure to the infectious stage of *C. shasta*. The size of experimental fish was determined chiefly by availability at the time they were needed. From data collected by Schaefer (1968) and Sanders et al. (1970), it was apparent that salmonids of a wide range of ages and sizes are susceptible to this pathogen. The Cowlitz fall chinook (*Oncorhynchus tshawytscha*) were obtained as eggs from the Washington Department of Fisheries, Cowlitz Salmon Hatchery. All other salmonid species and strains of chinook salmon were obtained from Oregon Department of Fish and Wildlife Hatcheries.

Exposure of fish to water containing the infectious stage is the only practical method of initiating ceratomyxosis (Schafer 1968; Sanders et al. 1970). The infectious stage of this parasite is present in the Willamette River when water temperatures exceed 10°C (Udey et al. 1975). All groups of fish were exposed in 0.074-m^3 cylindrical liveboxes placed in the Willamette River at Corvallis or Albany, Oregon.

To compare the susceptibility of the selected salmonid species (Table 1) the fish were exposed to

[1]Oregon Agricultural Experiment Station, Technical Paper No. 4413.

Printed in Canada (J4663)
Imprimé au Canada (J4663)

TABLE 1. Susceptibility of salmonids exposed to the infectious stage of *Ceratomyxa shasta* in the Willamette River in 1971 and 1972[a].

Year	Salmonid	Hatchery source[b]	No. fish exposed	No. fish recovered	No. dead fish infected with *C. shasta*
1971	Rainbow trout	Roaring River	50	50	50
	Cutthroat trout	Cedar Creek	50	47	47
	Brook trout	Fall River	50	50	50
	Atlantic salmon	Wizard Falls	50	30	0[c]
	Coho salmon	Fall Creek (Alsea)	50	50	21
	Spring chinook salmon	Marion Forks	50	47	5
	Sockeye salmon (kokanee)	Wizard Falls	50	49	2
1972	Cutthroat trout	Cedar Creek	56	51	51
	Brown trout	Ft. Klamath	50	49	10
	Fall chinook salmon	Trask River	58	58	54
	Chum salmon	Whiskey Creek	65	54	51

[a]1971 continuous exposure for 43 days from August 17 to September 29; 1972 continuous exposure for 66 days from August 1 to October 6. Temperatures ranged from 14.5 to 17°C and 12.5 to 21.5°C, respectively.

[b]The mean weight of fish used in these experiments ranged from 3 to 14 g.

[c]Nine fish (30%) became infected, however there were no deaths due to *C. shasta*. The 20 Atlantic salmon lost during the experiment are believed to have escaped through an opening in the livebox.

the infectious agent for prolonged periods. The exposure period extended for 43 days (August 17 to September 29) in 1971 and for 66 days (August 1 to October 6) in 1972. The water temperature ranged from 14.5 to 17°C in 1971 and from 12.5 to 21.5°C in 1972.

The susceptibility of hatchery strains of chinook salmon (Table 2 and 3) were compared using a prolonged exposure period of 86 days (June 16 to September 10, 1971) with temperatures ranging from 15 to 21°C. A short-term exposure period of 5 days similar to that of Udey et al. (1975) was also used where water temperatures ranged from 15.5 to 18.4°C. After the 5 day exposure these fish were transferred to the Oregon State University Fish Disease Laboratory and held at 18°C in 68-ℓ aquaria until termination 50 days later.

In addition to the presence of *Ceratomyxa*, the Willamette River is a reservoir for several bacterial fish pathogens. These potential infectious agents were anticipated and prophylactic measures undertaken to reduce their interference in these experiments (Udey et al. 1975). Terramycin in the form of TM_{50} (Pfizer) was incorporated at the 3% level into the Oregon Moist Pellet diet. This diet was fed daily beginning 8 days prior to exposure and continued until the termination of each experiment. There has been no evidence indicating Terramycin either enhances or inhibits the progression of ceratomyxosis in salmonids.

Dead fish were collected daily and wet mounts of intestinal scrapings examined microscopically (400×) for the presence of *C. shasta* spores (Udey et al. 1975). After terminating each experiment all surviving fish were examined in the same manner for sublethal infections. Among fish surviving at the termination of each experiment *C. shasta* was only found in the group of Atlantic salmon. No sublethal infections caused by the parasite were found in any other surviving fish. Since the incubation period before spores of *C. shasta* can be detected is rather long, approximately 15–25 days at the temperature ranges encountered for each experiment, some fish died of other causes before spores of the disease could be detected. These early deaths are reflected in the column of each table indicating the number of fish recovered. Only fish that survived this initial incubation period were considered in determining the relative susceptibility of each salmonid species or hatchery chinook strain. With few exceptions fish that died after the initial incubation period were infected with *C. shasta*. These observations, along with the characteristic disease symptoms (Schafer 1968), indicated that *C. shasta* was the prime cause of death.

Five infected fish from each species were examined in detail for the distribution of spores using wet mounts (400×) of tissue scrapings. The tissues and organs sampled were the stomach, ascending and descending intestine, liver, gallbladder, spleen, kidney, heart, gills, eyes, and epaxial muscles near the dorsal fin.

Results

SALMONID SPECIES

Brook trout (*Salvelinus fontinalis*), cutthroat trout (*Salmo clarki*), rainbow trout (*S. gairdneri*), chum salmon (*O. keta*), and fall chinook salmon were most highly susceptible to ceratomyxosis

based on percent mortality (Table 1). Coho salmon (*O. kisutch*) (42% mortality) were moderately susceptible. The brown trout (*Salmo trutta*), Atlantic salmon (*S. salar*), sockeye salmon (*O. nerka*) (kokanee), and spring chinook salmon exhibited the lowest mortalities (0–20%).

No deaths induced by *C. shasta* occurred in Atlantic salmon during the 43 day exposure period. However when the survivors were examined after terminating the experiment, spores were present in the intestines of nine fish (30%). Spores of *C. shasta* were not found in any other groups of surviving fish. This suggests that had the experiment been allowed to continue some Atlantic salmon may have eventually succumbed to this disease.

Five infected fish of each species were examined in detail for the distribution of spores in their tissues and organs. Spores were consistently found in all locations examined except the eyes and epaxial muscles of the moderately and highly susceptible salmonid species. Among the salmonids exhibiting the lowest levels of infection, spores were widely distributed only in the spring chinook salmon; in Atlantic and sockeye salmons and brown trout, spore distribution was limited. In Atlantic salmon, spores were found only in the ascending and descending intestine. In addition to the intestines, spores were also found in the stomach and spleen of brown trout and sockeye salmon.

Chinook Salmon Strains

Preliminary experiments by Johnson (1975) indicated strain differences of rainbow trout to susceptibility to ceratomyxosis. To test this further, groups of fall chinook salmon were exposed to the infectious stage of *C. shasta*.

The results of short-term (5-day) and long-term (86-day) exposures are shown in Tables 2 and 3, respectively. In both experiments the groups of fall chinook salmon from areas where the infectious stage of *C. shasta* does not occur, the Elk and Trask rivers, were considerably more susceptible (88–100% mortality) than the groups from areas where the parasite is naturally present (0–13% mortality). The Willamette and Carson hatcheries are located within the Columbia River basin. The Umpqua River arises from the western slope of the Cascade Range, but does not form part of the Columbia River basin. Each group of spring chinook salmon was more resistant to infection than the Trask River fall chinook salmon. These observations suggest that in spring chinook salmon stocks resistance to infection may be determined by factors other than prior exposure of the parental stocks to the infectious stage of *C. shasta*.

Table 2. Susceptibility of six hatchery stocks of chinook salmon (*Oncorhynchus tshawytscha*) exposed to the infectious stage of *Ceratomyxa shasta* in the Willamette River.[a]

Hatchery-stock chinook	No. fish exposed	No. fish recovered	No. dead fish infected with *C. shasta*
Columbia River basin			
Willamette spring chinook	90	90	2
Carson spring chinook	125	122	65
Bonneville fall chinook	125	121	0
Coastal rivers			
Umpqua spring chinook	125	123	25
Elk R. fall chinook	85	85	75
Trask fall chinook	125	123	123

[a]Temperature range during the 5 day exposure was 15.5–18.4°C. During the remainder of the experiment (50 days), fish were held in constant 18°C well water.

[b]The mean weight of fish used in these experiments ranged from 2 to 7 g.

Table 3. Susceptibility of four hatchery stocks of fall chinook salmon exposed to the infectious stage of *Ceratomyxa shasta* in the Willamette River.[a]

Harchery-stock fall chinook[b]	No. fish exposed	No. fish recovered	No. dead fish infected with *C. shasta*
Columbia River basin			
Big Creek	59	48	4
Cowlitz R.	65	53	3
Oxbow[c]	64	48	6
Coastal river			
Trask R.	50	42	40

[a]Exposed at Corvallis, Oregon for 86 days from June 16 to September 10, 1971, with a temperature range of 15–21°C.

[b]The mean weight of fish used in these experiments ranged from 3 to 7 g.

[c]On the Columbia River.

Discussion

All salmonid species used in these experiments proved susceptible to ceratomyxosis. However, the level of this susceptibility may vary widely among different strains of the same species of trout or salmon. This has been found for coho salmon (Schafer 1968; Sanders et al. 1970), brook trout (Wales and Wolf 1955; Schafer 1968), and chinook salmon (this paper). Wales and Wolf (1955) reported that brook trout were not susceptible to ceratomyxosis, while Schafer (1968) reported a low prevalence of infection (24% mortality). The brook trout strain exposed in this study was highly susceptible to *C. shasta* (100% mortality, Table 1). These findings suggest that brook trout may have strain resistance patterns similar to those of fall chinook salmon.

Results obtained with coho salmon have also varied widely. Schafer (1968) reported that Alsea River coho salmon were resistant, whereas 42% of our exposed fish succumbed to the parasite. Similarly, Schafer (1969) indicated that Klaskanine River coho salmon were resistant to infection, while Sanders et al. (1970) found *C. shasta* in 55% of the spawned adult coho salmon returning to this river.

Fall chinook salmon are usually considered to have a relatively low susceptibility to *C. shasta* infections (Sanders et al. 1970). In our experiments, both the long- and short-term exposures confirmed this opinion. However, those strains of fall chinook salmon that came from hatcheries located within the Columbia River basin were very resistant to ceratomyxosis. In contrast, hatchery strains derived from coastal rivers where the disease is not known to occur were highly susceptible to infection. The resistance developed by the Columbia River fish seems to be genetically transferred and was probably acquired by means of the selective advantage conveyed by resistance.

The studies with spring chinook salmon strains also suggest that resistance to infection may develop in stocks that have experienced no selective pressure from *C. shasta*. From fall chinook salmon exposures it could be expected that the Umpqua strain of spring chinook would be highly susceptible because the infectious stage of *C. shasta* has not been detected in this drainage system. However, upon exposure only 20% of these fish became infected. In contrast, the Carson strain, a native Columbia River stock, was expected to be resistant. However, 53% of these fish developed ceratomyxosis. Furthermore, Willamette spring chinook salmon which is very resistant to *Ceratomyxa* infections is a native stock that has long been able to adapt to this myxosporidan.

From data obtained in this study, it is not known why fish from the Umpqua drainage system are resistant to the infectious stage of *C. shasta*. Research should be continued with this and other salmonid species to compare different strain susceptibility. Geographical location may influence the prevalence of ceratomyxosis in other species of salmonids such as coho salmon and steelhead trout. The data indicate that resistance to infection by *C. shasta* is one of the major parameters that should be considered when introducing new salmonid strains or species into a drainage system that contains the infectious stage of this myxosporidan.

Acknowledgments

This work was supported by the Oregon Department of Fish and Wildlife under PI 89304 Anadromous Fish Act.

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Organochlorine Residues in Maternal Blubber, Milk, and Pup Blubber from Grey Seals (*Halichoerus grypus*) from Sable Island, Nova Scotia[1]

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ADDISON, R. F. AND P. F. BRODIE. 1977. Organochlorine residues in maternal blubber, milk, and pup blubber from grey seals (*Halichoerus grypus*) from Sable Island, Nova Scotia. J. Fish. Res. Board Can. 34: 937–941.

Residues of DDT group insecticides and of PCBs were measured in samples of maternal blubber, milk, and pup blubber from grey seals (*Halichoerus grypus*) from Sable Island, N.S. Mean ΣDDT and PCB levels in maternal blubber lipid were 14.0 and 14.5 μg/g, respectively. Concentrations of DDT and PCBs in milk lipid were approximately 60 and 30%, respectively, of those found in maternal blubber lipid, suggesting a partial barrier to passage of these residues through mammary tissue. Concentrations in pup blubber lipid were the same as, or slightly higher than, those in milk lipid.

We estimated that a grey seal will lose about 30% of its total ΣDDT burden and about 15% of its PCB burden through lactation; this would be approximately balanced by its estimated annual intake of these residues from food. Thus, the observation that female seals show no increase in residue burdens with age (in contrast to males) is explained.

Key words: organochlorine, DDT, DDE, PCB, seal, blubber, milk

ADDISON, R. F., AND P. F. BRODIE. 1977. Organochlorine residues in maternal blubber, milk, and pup blubber from grey seals (*Halichoerus grypus*) from Sable Island, Nova Scotia. J. Fish. Res. Board Can. 34: 937–941.

Nous avons mesuré les résidus d'insecticides du groupe DDT et de BPC dans des échantillons de graisse maternelle, de lait et de graisse de chiots de phoques gris (*Halichoerus grypus*) de l'île de Sable, N.-E. Les niveaux moyens de ΣDDT et de BPC dans les lipides de la graisse maternelle sont respectivement de 14.0 et 14.5 μg/g. Les concentrations de DDT et de BPC dans les lipides du lait sont d'environ 60 et 30% respectivement de celle que l'on trouve dans les lipides de la graisse maternelle, ce qui suggère la présence d'une barrière partielle au passage de ces résidus à travers le tissus mammaire. Les concentrations dans les lipides de la graisse des chiots sont les mêmes ou légèrement plus élevées que celles des lipides du lait.

On estime qu'un phoque gris perd environ 30% de sa charge totale de ΣDDT et environ 15% de sa charge de BPC durant la lactation; ceci serait approximativement contrebalancé par l'absorption annuelle estimée de ces résidus en provenance de la nourriture. On peut donc expliquer de cette façon l'observation que les phoques femelles ne montrent pas d'augmentation dans les charges de résidus avec l'âge (par contraste avec les mâles).

Received December 10, 1976
Accepted March 10, 1977

Reçu le 10 décembre 1976
Accepté le 10 mars 1977

ORGANOCHLORINE residue concentrations in male seals increase with the animal's age. The connection is well established for harp seals (*Pagophilus groenlandicus*) from the Gulf of St. Lawrence (Addison et al. 1973) and ringed seals (*Pusa hispida*) from the Canadian arctic (Addison and Smith 1974). This relationship is not observed, however, in female ringed seals from the arctic (Addison 1973; Addison and Smith 1974) or the Baltic (Helle et al. 1976). This suggests that female seals can excrete organochlorine residues by some route(s) closed to the male, the most obvious being parturition and/or lactation. In fact, organochlorine residues are found in the milk of fur seals and, though only in traces, in their fetuses (Anas and Wilson 1970). This implies that lactation may be a major route of excretion in marine mammals, and this view is supported by analyses showing that residue concentrations in pregnant and/or lactating female porpoises are generally lower than those in immature or resting animals (Gaskin et al. 1971).

If female seals do not increase their residue burdens as they grow older, quite large amounts

[1]Bedford Institute of Oceanography Contribution.

Printed in Canada (J4664)
Imprimé au Canada (J4664)

of residues must be excreted in milk. To estimate these quantities, we have measured residue levels in milk lipid from grey seals and compared them with those in maternal blubber lipid. Residues in blubber lipid of pups fed on the milk were also measured.

Materials and Methods

Five isolated pairs of mother and pup grey seals (*Halichoerus grypus*) were sampled on Sable Island, N.S., in January 1974; a second group of six pairs was sampled in January 1976. Cores of blubber were taken from the middorsal region and stored in plastic bags. Milk samples were obtained from the mother by slicing mammary tissue and collecting the exudate in a glass vial; occasionally these samples were slightly discolored with blood. Samples were stored at ambient temperature (approximately −5°C) for 3 days, and on return to Dartmouth were frozen for some weeks at −20°C until analyzed.

Lipid was extracted from a 10-g blubber sample, dissected from the interior of the core, and from as much milk as was available (usually around 5 ml) by the method of Folch et al. (1957). Lipid was determined gravimetrically on an aliquot of the extract. Organochlorine residues were analyzed generally as described previously (Addison et al. 1972).

Results and Discussion

Sizes of the animals examined and lipid contents of blubber and milk samples are summarized in Table 1. As indicated by the pelage and measurements of the girth and blubber thickness, all the pups in the 1974 samples were at stages 1, 2, or 3 (based on the system used by the laboratories within Department of Fisheries and the Environment). These correspond (approximately) to 0–4, 5–10, and 11–15 days old, respectively. In the 1976 samples the pups ranged from stages 2 to 4, stage 4 corresponding to the start of molting. Young seal pups have a phenomenal growth rate and this must depend on the amount of milk ingested. None of the pups had been weaned. Mother seals in the 1976 samples ranged in age from 5 to 8 yr old.

Lipid content of maternal blubber ranged from approximately 75–90% fresh wt. Pup blubber lipid was in the approximate range 70–90% fresh wt, and in younger animals (stage 1 and 2) was usually slightly lower than maternal blubber lipid content; in stage 3 and 4 pups it was the same as, or slightly higher than, that in maternal blubber. All these data are similar to those reported by other authors for similar samples (e.g. Ackman and Burgher 1963; Jangaard and Ke 1968; Addison et al. 1973).

Of the DDT group of insecticides, only *p,p'*-DDE and *p,p'*-DDT were present in sufficient quantity to allow reliable estimation. A peak corresponding to *p,p'*-DDD was also present but was small and overlapped with PCB components. No attempt was made to analyze PCBs in the 1974 series of samples, but they were quantified (with the usual reservations: Addison et al. 1973) in the 1976 samples. Somewhat unexpectedly in comparison with our previous analyses (Addison et al. 1973; Addison and Smith 1974) of PCBs in seal samples, the pattern corresponded better to that of Aroclor® 1260 than of Aroclor® 1254.

Organochlorine residue concentrations are summarized in Table 2. In general, total DDT group residues (ΣDDT) were in the approximate ranges 7–30 μg/g (maternal blubber lipid), 3–16 μg/g (milk lipid), and 4–13 μg/g (pup blubber lipid). PCB concentrations (1976 samples only) were in the approximate range 7–25 μg/g (maternal blubber lipid), 1–6 μg/g (milk), and 1–3 μg/g (pup blubber lipid). These ranges are generally similar to those reported elsewhere (where samples are comparable) for eastern Canadian seals (Holden and Marsden 1967; Holden 1970; Addison et al. 1973). As expected from our earlier work (Addison and Smith 1974), residue concentrations in the 1976 maternal blubber samples were not well correlated with the age of the animals; linear regressions of ΣDDT and PCB concentrations on age showed correlation coefficients (r) of 0.17 and 0.47, respectively.

Approximately 60% of ΣDDT was in the form of *p,p'*-DDE. This ratio was virtually constant for milk and blubber samples taken in either 1974 or 1976 and is similar to that reported previously (Addison et al. 1973).

In milk lipid, ΣDDT concentrations were lower than those in maternal blubber lipid. ΣDDT concentrations in milk lipid represented only 56.4 ± 17.1% (mean ± SD) of those in maternal blubber lipid in the 1974 samples; comparable figures for 1976 were 64.7 ± 13.9%. Differences between 1974 and 1976 are not statistically significant by t-test. In the 1976 samples PCB concentrations in milk lipid were only 34.0 ± 17.5% of those in maternal blubber lipid. The difference between the transfer of DDT group and that of PCBs from maternal blubber lipid to milk lipid (1976 samples) is significant by t-test ($P < 0.01$). The difference implies a restriction of the passage of PCBs through mammary tissue relative to passage of the DDT group.

The lower organochlorine residue concentrations in milk lipid compared to those in maternal blubber could arise for several reasons. There may be some selectivity in the mobilization of lipid from blubber, which could result in dilution

TABLE 1. Size, lipid content, and stage of development of Sable Island grey seals (1974 and 1976).

Sample no.	Length (cm)	Girth (cm)	Blubber thickness (mm)	Development stage and sex of pup	% Lipid content	
					Blubber	Milk
1974						
Mother } A	195	157	40		88.0	48.6
Pup } A	105	75	18	1, M	71.8	—
Mother } B	203	156	37		92.7	43.3
Pup } B	104	66	10	1, F	73.0	—
Mother } C	205	150	35		86.3	34.5
Pup } C	102	92	45	3, F	89.0	—
Mother } D	192	142	40		92.8	52.3
Pup } D	98	83	27	2, M	88.3	—
Mother } E	199	137	34		87.7	53.4
Pup } E	116	80	25	2, M	82.6	—
1976						
#10 Mother	180	130	43		90.6	55.1
#10 Pup	109	75	22	2, F	81.9	—
#11 Mother	184	127	50		88.6	46.0
#11 Pup	95	71	27	2, F	80.5	—
#12 Mother	201	128	42		77.8	59.4
#12 Pup	107	90	31	2, M	83.1	—
#13 Mother	181	111	23		74.6	44.4
#13 Pup	116	96	57	4, F	80.3	—
#14 Mother	183	120	36		80.1	59.8
#14 Pup	115	94	39	3, F	87.5	—
#15 Mother	170	109	25		82.0	51.3
#15 Pup	110	99	47	4, F	86.0	—

TABLE 2. Residues of *p,p'*-DDT, *p,p'*-DDE and PCBs as Aroclor® 1260 (1976 samples only) in micrograms per gram lipid from Sable Island grey seals (1974 and 1976). (Arranged by year in order of increasing pup development.) ND = not determined; MB = maternal blubber; PB = pup blubber.

Sample	Age of mother (yr)	Pup stage	*p,p'*-DDT			*p,p'*-DDE			ΣDDT			PCBs		
			MB	Milk	PB	MB	Milk	PB	MB	Milk	PB	MB	Milk	PB
1974														
B	ND	1	4.1	2.2	3.1	5.0	3.3	4.4	9.1	5.5	7.5	ND	ND	ND
A	ND	1	3.9	1.4	1.7	4.5	2.0	2.5	8.4	3.4	4.2	ND	ND	ND
E	ND	2	8.3	3.2	4.2	9.6	4.9	6.2	17.9	8.1	10.4	ND	ND	ND
D	ND	2	9.7	4.6	4.0	7.9	4.8	6.5	17.6	9.4	10.5	ND	ND	ND
C	ND	3	1.8	2.5	3.4	5.0	3.2	5.4	6.8	5.7	8.8	ND	ND	ND
1976														
10	5	2	3.4	2.4	3.0	7.3	3.5	4.3	10.7	5.9	7.3	7.1	1.3	1.6
11	8	2	4.2	1.9	2.3	6.5	4.0	4.0	10.7	5.9	6.3	11.7	3.1	3.0
12	7	2	12.6	5.9	5.4	18.6	10 0	8.5	31.2	15.9	13.9	24.6	5.7	3.2
14	8	3	5.0	4.3	1.9	8.6	5.0	4.3	13.6	9.3	6.9	18.2	4.6	3.0
15	7	4	9.5	7.3	1.7	8.4	8.4	3.8	17.9	15.7	5.5	12.1	7.6	1.5
13	6	4	4.1	2.2	1.7	5.8	4.8	2.4	9.9	8.0	4.1	13.4	6.4	1.4

of the residue concentrations in lipid reaching the mammary tissue, but we know of no evidence to support this. Our analyses (R. F. Addison and J. Dale unpublished data) indicate no obvious stratification of organochlorine residue distribution within blubber that could account for such selectivity. A second possibility is that residue concentrations in milk lipid may be diluted by de novo lipid synthesis in mammary tissue. Although mammary tissue of other mammals is metabolically active in lipid synthesis (e.g. Patton and Jensen 1976), we do not know of any studies of the functions of mammary tissue in seals. A third possible explanation of the dilution in organochlorine residues in milk as compared to those in maternal blubber is that there may be

a physiological barrier at the mammary tissue that prevents quantitative transfer of residues. To judge by the comparisons of ΣDDT and PCB levels in milk (Table 2) such a barrier (if it exists) is more effective in restricting PCB passage into milk.

Residue concentrations in pup blubber lipid were generally similar to or slightly higher than those in milk lipid and approximately half the concentrations in maternal blubber. Similar ratios were reported by Heppleston (1973). If pups were selectively catabolizing some of the ingested lipid for energy purposes, while retaining the burden of residues ingested along with the milk, residue concentrations in their blubber lipid should have been slightly higher than those in milk lipid. Although this was true of the younger pups (stages 1, 2, and sometimes 3), it certainly did not hold for the older pups (Table 2). In these animals residue concentrations in blubber lipid were appreciably below those in milk. This is surprising, since these older animals (stage 4) either are terminating milk feeding or are starving, but are not yet weaned. We would expect that residue concentrations in the blubber lipid of such animals would increase to levels well above those in milk lipid, whereas our analyses suggest that some dilution apparently took place. This trend is reasonably consistent over the two sampling periods. At present we can offer no explanation for it.

We can construct a ΣDDT balance for the lactating grey seal using data presented here and taken from elsewhere in the literature. A typical 170-kg lactating grey seal may lose about 44 kg during a 15-day lactation (Amoroso et al. 1961; Amoroso and Matthews 1951). If most of this weight loss was blubber we can assume a total blubber loss of, in round figures, 40 kg blubber lipid. Assume this contains ΣDDT at a mean concentration of 14 μg/g, of which 60% is transferred to milk (mean values of present data). Total ΣDDT loss during lactation by Sable Island grey seals is then:

$$4 \times 10^4 \times 0.6 \times 1.4 \times 10^{-5} = 336 \text{ mg } \Sigma\text{DDT}.$$

A mature grey seal will eat about 1×10^6 – 1.5×10^6 g biomass in the course of a year (estimates from observations on wild and captive animals by P. F. Brodie). This would be mainly herring, cod, flounder, etc. (Mansfield 1966), and in eastern Canada, the concentration of ΣDDT residues at this trophic level would be about 0.1–0.5 μg/g wet wt (e.g. Zitko 1971; Addison et al. 1972; Sims et al. 1975). The range of total DDT ingested would therefore be:

$$(1 \times 10^6 \text{ to } 1.5 \times 10^6) \times (0.1 \text{ to } 0.5) \times 10^{-6} = 100 \text{ to } 750 \text{ mg } \Sigma\text{DDT}.$$

The mean annual estimated ΣDDT intake (425 mg) is impressively close to the amount excreted during lactation. It is therefore not surprising that ΣDDT concentrations in lactating females should show no appreciable increase with age, since loss during annual reproduction (Mansfield 1966) approximately balances annual uptake from feeding.

Similar calculations for PCBs, using data from sources referred to above, suggest a net excretion of PCBs from lactating Sable Island grey seals of about 200 mg. Annual intake would be around 300 mg, and so PCB residue concentrations in such seals are approximately in equilibrium with their dietary sources.

In more general terms, the 40 kg or so blubber lipid mobilized by the grey seal during lactation represents about half her total lipid reserves. Since the efficiency of transfer of ΣDDT to milk is about 60%, the female will lose about 30% of her total residue burden in any one lactation, assuming that all her residue burden is stored in blubber. This 30% is about equal to the percentage that any one year's food intake at maturity represents of total food intake up to then. Assuming that residue concentrations in food were constant over her life span, annual uptake and loss of residues should be about equal during her reproductive years.

Our calculations therefore strongly support our view that lactation is a major route for excretion of organochlorine residues by seals.

Acknowledgments

We thank Mr M. E. Zinck and Mrs J. Dale for performing some of the analyses. The ages of the 1976 adult samples were determined by staff of the Arctic Biological Station, Ste Anne-de-Bellevue, Quebec.

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Dynamics of an Exploited Population of Lake Whitefish (*Coregonus clupeaformis*)

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BELL, G., P. HANDFORD, AND C. DIETZ. 1977. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*). J. Fish. Res. Board Can. 34: 942–953.

The life history of the exploited lake whitefish (*Coregonus clupeaformis*) population of Lesser Slave Lake, Alberta, is described. Mean age is high, having increased under continued exploitation during the last 30 yr. A method of estimating the population age structure is described. The apparent annual rate of survival of adult fish has fluctuated markedly, but on average seems to lie in the interval 0.40–0.50; the annual rate of natural survival is estimated to be 0.53. Juveniles survive better than adults. Rate of survival during the 1st yr of life was estimated to be about 0.0002. Maturity was late, the median age at first reproduction being 6–6$^1/_2$ yr. The regressions of fecundity on age and length are described; length now contributes almost all the attributable variance to maturity and fecundity. The sex ratio fluctuates in time; this is caused by the fluctuations in age structure, since sex ratio varies with age. The relationship between sex ratio and age is used to calculate the relative rates of survival of male and female fish.

These data are used to construct a life table and to compute population parameters. It is inferred that the ability of the population to respond to exploitation has been eroded during the last 30 yr. In some respects, the life history of the Lesser Slave Lake stock appears to be unusual.

After about 30 yr of large-amplitude oscillation the whitefish population collapsed in 1965. This does not seem to have been caused by chronic overfishing. In the first place, the rate of fishing mortality is no more than moderate. Secondly, a multiple regression equation describing whitefish catch in 48 other Alberta lakes in which there has been no overall decline in catch successfully predicts the observed mean catch at Lesser Slave Lake. The oscillations in catch are claimed to reflect a limit cycle in the abundance of the whitefish, driven by a lagged relationship between a predator (the fishermen) and its prey (the whitefish). Whether or not this cycle was deterministically stable, such behavior will inevitably put the population in risk of extinction during troughs in the cycle. We suggest that current management policies may encourage the destabilization of whitefish populations, and we propose a remedy.

Key words: population dynamics, population regulation, life history, exploitation, survival, fecundity, *Coregonus clupeaformis*

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Nous décrivons le cycle biologique d'une population exploitée de grands corégones (*Coregonus clupeaformis*) du Petit lac des Esclaves, Alberta. L'âge moyen est élevé, ayant augmenté à la suite d'une exploitation continue au cours des 30 dernières a. Nous décrivons une méthode d'estimation de la distribution des âges dans la population. Le taux annuel apparent de survie des adultes accuse de grandes fluctuations, mais il semble se situer en moyenne dans l'intervalle de 0.40–0.50; on estime à 0.53 le taux annuel de survie naturelle. Les jeunes survivent mieux que les adultes. On estime à environ 0.0002 le taux de survie durant la première année. La maturité est tardive, la médiane d'âge à la première reproduction étant de 6–6$^1/_2$ ans. Nous donnons les régressions de la fécondité sur l'âge et la longueur; la longueur contribue présentement presque toute la variance attribuable à la fois à la maturité et à la fécondité. La proportion des sexes varie dans le temps; cela est dû aux fluctuations de la répartition des âges, étant donné que la proportion des sexes varie avec l'âge. On utilise la relation entre la proportion des sexes et l'âge pour calculer les taux relatifs de survie des mâles et des femelles.

A partir de ces données, nous construisons une table de mortalité et calculons les paramètres de la population. On en déduit que l'aptitude de la population à répondre à l'exploitation s'est érodée au cours des 30 dernières a. Sous certains aspects, le cycle biologique du stock du Petit lac des Esclaves semble inusité.

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Printed in Canada (J4277)
Imprimé au Canada (J4277)

Après environ 30 ans d'oscillations de forte amplitude, la population de grands corégones s'affaissa en 1965. Ceci ne semble pas avoir été causé par une surexploitation chronique. En premier lieu, le taux de mortalité causée par la pêche n'est pas plus que modéré. En second lieu, une équation de régression multiple décrivant les prises de grand corégone dans 48 autres lacs de l'Alberta, où les prises en général n'avaient pas diminué, permet de prédire avec succès la prise moyenne observée dans le Petit lac des Esclaves. On prétend que les oscillations dans les prises reflètent un cycle limite dans l'abondance du grand corégone, actionné par une relation décalée entre un prédateur (les pêcheurs) et sa proie (le grand corégone). Que ce cycle soit ou non stable par déterminisme, un tel comportement fera inévitablement courir à la population le risque d'extinction quand le cycle passe par des creux. Nous suggérons que les politiques de gestion courantes peuvent être de nature à encourager le déséquilibre des populations de grands corégones, et nous proposons un remède.

Received April 5, 1976
Accepted March 10, 1977

Reçu le 5 avril 1976
Accepté le 10 mars 1977

Lesser Slave Lake is a mesotrophic lake, about 1200 km^2 in area and no more than 18.6 m deep, in central Alberta. It has supported a fishery for lake whitefish (*Coregonus clupeaformis*) since the late 19th century. The history of the fishery has on the whole been one of decline, culminating in the collapse of 1965, after which the fishery was closed for several years. A certain amount of biological data had been accumulating since the pioneer efforts of R. B. Miller in the 1940s, and the collapse in the mid-1960s resulted in the inauguration of a much larger program of research. This paper is the first to come from this program, and describes and interprets the life history and population dynamics of the whitefish.

Life History

Age Structure

Scales were used to determine age. All available material was reread by one of us (C.D.). Until 3 or 4 yr of age, scale annuli were found to be clearly defined by the first wide circulus following a series of narrow, closely spaced circuli. In older fish the annuli were less distinct, and the criteria used in reading scales were, in order of importance: the "cutting-over" of circuli into the lateral fields, the resorption of circuli, a break in the pattern of circuli indicated by a discontinuity, and the spacing of annuli. Until the 1960s the scales are easily read, and reexamination of the older material gave results in good agreement with those recorded at the time of sampling. In recent years the scales have become more difficult to read, but there is independent evidence that our estimates of age are satisfactory. First, the length-frequency distributions enable the fish in the first two or three year-classes to be identified independently; this identification confirms the scale readings. Secondly, the sectioning of pelvic fin-rays yields the same estimates of age as scale reading in most cases (40/64); the mean difference between the two estimates was <½ yr, and the differences were symmetrically distributed in a binomial fashion about zero. Finally, since strong year-classes can be traced in subsequent years (Handford et al. 1977, table 1), the periodicity of ring formation must be annual.

The mean age of samples caught in gill nets (5–5½ in. stretched measure) by test gangs and by the commercial fishery between 1941 and 1975 has increased considerably (Handford et al. 1977, fig. 1). Although the age structure of the catch has been influenced by a number of dominant year-classes, the procession of these dominant year-classes through the population is not a sufficient explanation of the long-term upward trend in mean age.

The sample age structure is a statistic of limited usefulness, since it depends not only on rates of mortality and natality, but also on the ages at which the fish enter the exploited stock (Ricker 1975). The age structure of the whole population would be more useful if it could be measured. It cannot be measured directly because no one has yet succeeded in designing gear that will simultaneously catch individuals of all ages with equal efficiency, but it can be estimated indirectly as follows: let the number of fish caught per unit effort with gear of "size" (e.g. mesh size) g be $N(g)$. Then $N = \int_0^w N(g)\, dg$, where N is the total number of fish caught when gear of all sizes is fished with unit effort and w is the size of gear above which the catch is zero (about 6 in. in Lesser Slave Lake). Let the frequency of fish aged x caught in gear of size g be $f(x,g)$. Then the total number of fish aged x among the catch of gear of size g is $N(g)\ f(x,g)$, and the total number of fish aged x caught when gear of all sizes is fished simultaneously with unit effort is $N(x) = \int_0^w N(g)\ f(x,g)\ dg$. An estimate of the frequency of fish aged x in the population as a

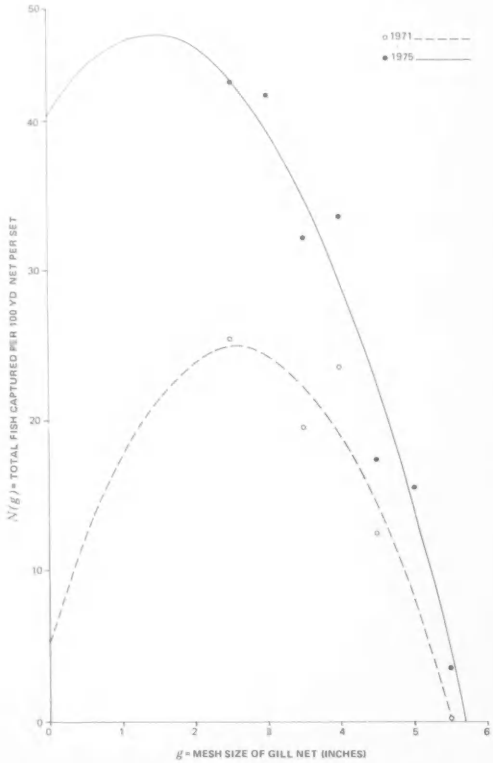

FIG. 1. Curves of $N(g)$ vs. g for 1971 and 1975, used in calculating the population age structure. $N(g)$ is the number of individuals caught when gear of size g is fished with unit effort. Equations of machine-fitted second-order polynomials are:

1971: $N(g) = 5.36 + 15.02g - 2.89g^2$
1975: $N(g) = 40.39 + 7.22g - 2.50g^2$

whole is then:

$$c(x) = N(x)/N = \int_0^w N(g)f(x,g)dg \Big/ \int_0^w N(g)dg$$

We find empirically that $N(g)$ can be represented by a second-order polynomial and $f(x,g)$ by a third-order polynomial (Fig. 1 and 2). Given the coefficients of these polynomials, the definite integrals are easily solved. This procedure cannot be followed for the 0+ class, which was estimated as $c(0) = \sum^{x=w} c(x)\ F(x)\ b(x)$, where $F(x)$ and $b(x)$ are the age-specific schedules of maturity and fecundity, respectively (discussed below). Figure 3 shows the calculated population age

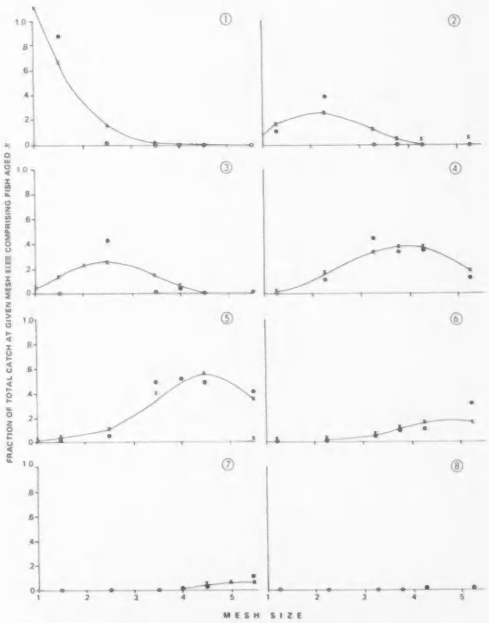

FIG. 2. Curves of $f(x,g)$ vs. g for 1971, used in calculating the population age structure. Here, $f(x,g)$ is the frequency of fish aged x among all those caught by gear of size g. Solid circles are raw data. Equations of machine-fitted third-order polynomials are:

$f(1,g) = 2.38 - 1.61g + 0.35g^2 - 0.025g^3$
$f(2,g) = -0.80 + 1.10g - 0.35g^2 + 0.0315g^3$
$f(3,g) = -0.82 + 1.05g - 0.32g^2 + 0.028g^3$
$f(4,g) = 0.061 - 0.22g + 0.15g^2 - 0.020g^3$
$f(5,g) = 0.54 - 0.87g + 0.38g^2 - 0.042g^3$
$f(6,g) = 0.34 - 0.46g + 0.165g^2 - 0.016g^3$
$f(7,g) = 0.11 - 0.14g + 0.048g^2 - 0.004g^3$
$f(8,g) = 0.015 - 0.020g + 0.007g^2 - 0.0007g^3$

structures in 1971 and 1975, the only 2 yr for which sufficient data are available.

SURVIVAL

Estimates of the age structure are the only data available for the Lesser Slave Lake whitefish from which rates of survival can be calculated. A large collation of recipes for calculating survival rates from "catch curves," i.e. from the descending limb of the sample age structure, has been given by Ricker (1975). The age structures of the 5–5½-in. gill net samples from Lesser Slave Lake were treated in two ways. When pooled for all years, the data are best linearized by a semilogarithmic regression, implying a constant annual rate of survival in adult fish (Fig. 4). The

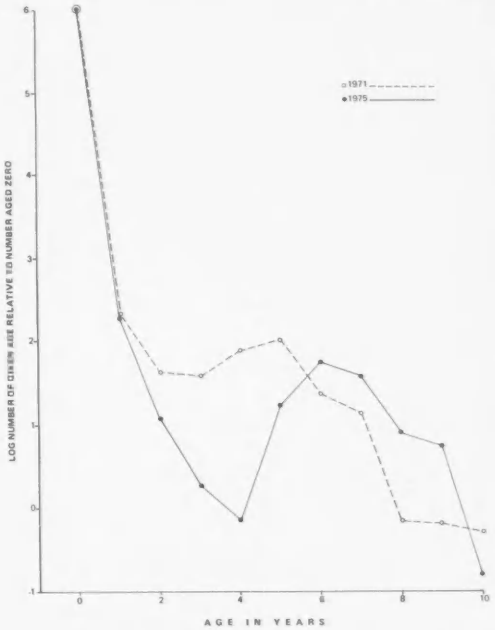

FIG. 3. Population age structures in 1971 and 1975.

slope of this regression indicates an average annual rate of survival of 0.471. Alternatively, we may obtain separate estimates of survival for each year; the geometric mean of these estimates is 0.371. This is a horizontal estimate, obtained by regressing the numbers of individuals of given age in a given year against age; the corresponding diagonal estimate would be made by regressing the number of individuals in a given cohort against age. The geometric mean of the diagonal estimates is 0.446.

The population age structures in 1971 and 1975 can also be manipulated to yield estimates of survival. The number of 1-yr fish as a fraction of the number of 0-yr fish was almost the same in the 2 yr of sampling: 0.00019 and 0.000205, respectively. The average of these two numbers, 0.0001975, is thus probably a reasonable estimate of the rate of survival during the 1st yr of life. Rates of survival at other ages can be computed from the relationship:

$$s(x, x+1, t) = \lambda^y \, c(x+1, t)/c(x, t-y)$$

where λ is the finite rate of increase per year, calculated from the observed rate as $(\int_0^\infty N(g,1975)\, dg / \int_0^\infty N(g,1971)\, dg)^{1/4} = 1.195$, and $s(x, x+1, t)$ is the rate of survival between ages x and $x+1$

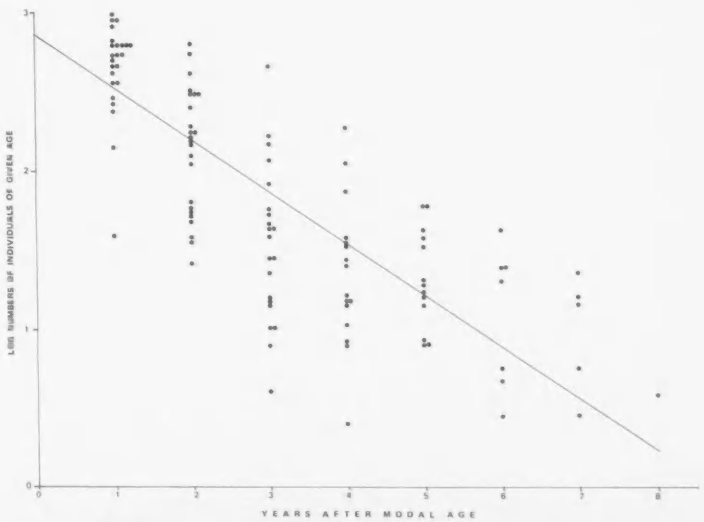

FIG. 4. Semilogarithmic regression of descending limb of age structures; pooled data from 1941 to 1974 5–5½-in. gillnet samples. Regression equation is: $\log N(x) = 2.847 - 0.327x$, where $N(x)$ is the number of individuals aged x years older than the modal age $N(0)$ of the sample, relative to $N(0) = 1000$. The regression has $r^2 = 0.719$.

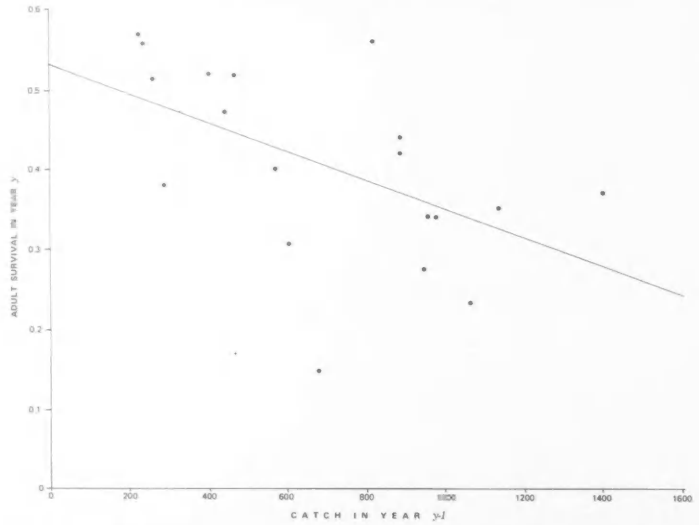

FIG. 5. Relationship between annual rate of adult survival (p) in year (y) and total catch in millions of pounds (C) in year (y-1). Regression equation is: $p = 0.533 - 0.182C$, with $r = 0.53$, $0.01 < P < 0.05$.

that has been experienced by fish living at time t. This procedure yields annual rates of "juvenile" survival (fish aged between 1 and 7 yr) of 0.627, and of "adult" survival (fish aged between 7 and 10 yr) of 0.509.

Rates of survival calculated from the sample age structures vary considerably from year to year, but this is at least partly caused by the trends in age structure described above. However, there is a suggestive negative relationship between catch and apparent adult survival (Fig. 5). The y-intercept of this diagram is an estimate of the natural survival rate (0.533), which is not much larger than the estimate of adult survival in 1971–75, when fishing pressure was unusually light. The x-intercept of the same regression is an estimate of the total weight of fish in the catchable segment of the population. This estimate is about 3×10^6 pounds (1 pound, avdp, = 453.59 g), indicating a population number of roughly 1.5×10^6.

AGE AT MATURITY

Frequency of mature fish at given age can be described by a number of distributions, including the cumulative normal distribution. However, the simplest is the logistic form:

$$F(x) = \frac{F(w)}{1 + \exp[-k(x - x^*)]}$$

where $F(x)$ is the frequency of mature fish among all fish aged x, $F(w)$ is the frequency of mature fish among the oldest age groups, x^* is the age at the point of inflection of the curve, and k is a constant governing the steepness of the curve. To facilitate fitting a regression by least squares, this expression was linearized as:

$$\ln (1/F(x) - 1) = -k(x - x^*)$$

by taking $F(w) = 1$. Results are shown in Fig. 6; at ages greater than those shown on the diagram, all individuals are mature. The median age at maturity is 6 yr or greater. There is no considerable difference between the sexes, but females appear to mature slightly earlier than males, an unusual observation.

Mature fish of given age are considerably larger than immature fish of the same age (Fig. 7). Moreover, there is virtually no overlap in length between the youngest mature fish and the oldest immature fish. This suggests that maturity is reached at a given size, irrespective of age, and that the schedule of maturity is properly size specific rather than age specific. Figure 7 also shows that the rate of growth of immature fish is greater than that of mature fish, which is to be expected if reproduction implies a withdrawal of energy from somatic growth. However, the finding that this reduction in growth is about the same for males as it is for females is unexpected.

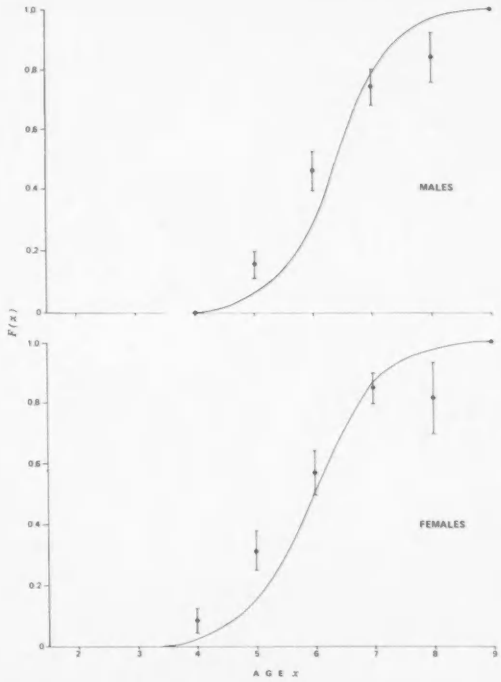

FIG. 6. Schedules of maturity (1974 data). $F(x)$ is the frequency of mature fish among all fish aged x; curves fitted as explained in text. Parameters are estimated as follows: females $k = 2.30$, $x^* = 6.43$ ($r^2 = 0.90$); males $k = 1.85$, $x^* = 5.97$ ($r^2 = 0.89$).

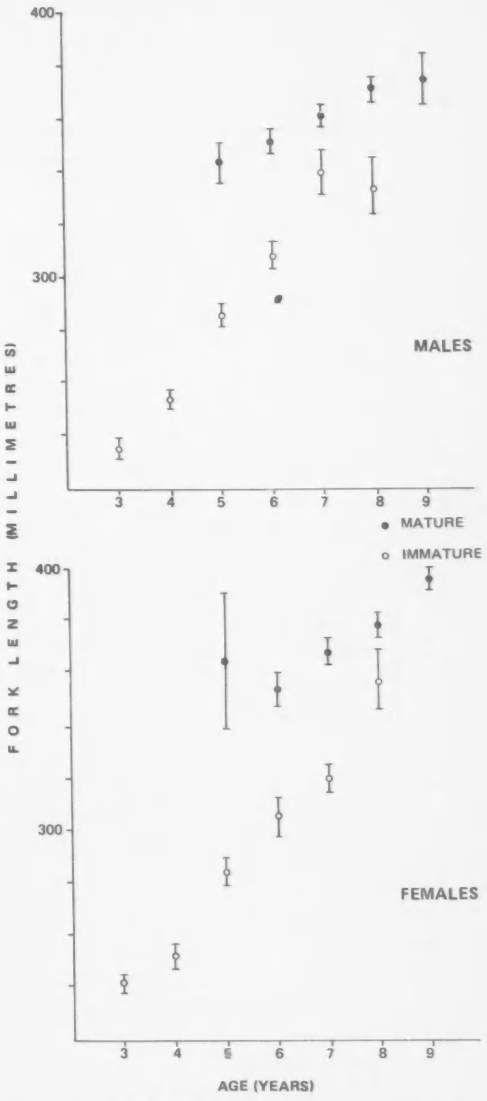

FIG. 7. Length and age at maturity. Data plotted as mean ± 1 SE. Data from two trawl samples taken in August 1974.

FECUNDITY

We weighed 1000 air-dried eggs from each fish as a basis for estimating total egg number per fish. In each of six experiments the estimate was <1% different from the number of eggs determined by total count. Only females in which the ovaries appeared to be intact were used. The regressions of fecundity on length and age were found to be satisfactorily linearized by a $\log_{10}$ transformation of fecundity (Table 1A), although a very small further improvement can be achieved by logging the x-variable also. There were no significant differences between the parameters of these regressions in different years. Stepwise regression shows that age plays little part in the determination of fecundity, all or almost all of the explained variance being contributed by variance in length (Table 1B).

SEX RATIO

The sex ratio of the samples from 5–5½-in. gill nets fluctuated markedly with time between 1944 and 1974 (Fig. 8). Moreover, the sex ratio at any given time was correlated with the mean age of fish in the population (Fig. 9). Both observations are explained by the changing frequency of the sexes with age (Table 2). Males predominate up to age 5; females are more common from age 7

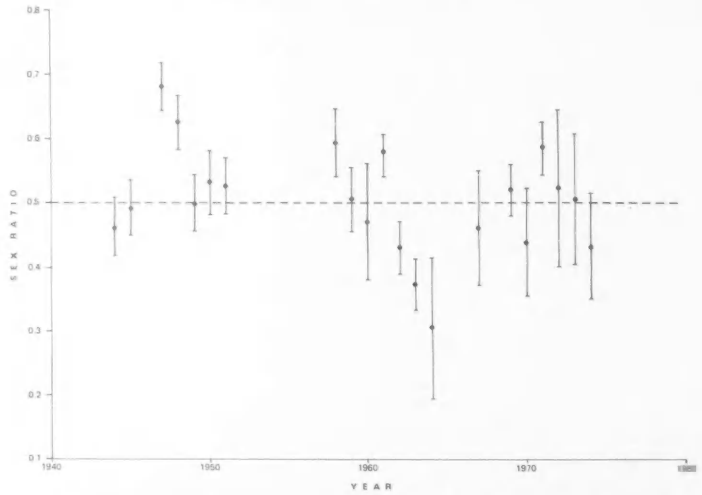

FIG. 8. Fluctuations in sex ratio with time, 1941–74. Data plotted as mean (males/total), with 95% confidence limits indicated.

TABLE 1. A, Linear regression of $\log_{10}$ fecundity on length and age in 3 separate yr. N is the number of fish in the sample (length range 38–51 cm only), b_0 the intercept, b_1 the slope coefficient, and r the correlation coefficient. B, Multiple correlation coefficients, R, from stepwise regression of $\log_{10}$ fecundity on length and age.

		1971	1974	1975
A				
Fork length	N	56	150	95
(mm)	b_0	2.929	2.517	2.474
	b_1	0.003	0.005	0.005
	r	0.632	0.805	0.802
Age,	b_0	3.633	3.947	3.900
(yr)	b_1	0.089	0.051	0.059
	r	0.492	0.403	0.416
B				
Length	R	0.632	0.805	0.802
Age and length	R	0.662	0.805	0.802

onwards. Given an equal primary (egg) sex ratio and nearly equal rates of growth, this implies that males mature earlier in life (or are exposed to the fishery earlier) but suffer a greater mortality as adults. In recent years, as shown above, males and females mature at about the same age, but this may not have been true during the earlier part of the period over which the data for Table 2 was collected. Since the sex ratio changes markedly with age, for whatever reason, the pronounced fluctuations in age structure referred to above will generate the fluctuations in the sex ratio shown in Fig. 8.

Monotonic changes in sex ratio with age such as those described above provide a means of estimating the ratio of male to female rates of survival. We define seven variables: a^* is the first possible age at maturity, a is the mean age at maturity, w is the age at last reproduction, s is the rate of survival to age a^*, c is the annual rate of survival between ages a^* and a, p is the annual rate of survival between ages a and w, and $R(x)$ is the ratio of males to females at age x. Further, let the subscripts m and f refer to males and females, respectively. Suppose that $p_m = k_1\ p_f$ and $a_m = a_f - k_2$ so that k_1 and k_2 are parameters that equate survival and maturity in the two sexes. Then from first principles we have:

$$R(x) = \frac{s \cdot c^{a_f - a^* - k_2} \cdot (k_1 p_f)^{x - a_f - k_2}}{s \cdot {}^s c^{a_f - a^*} \cdot {p_f}^{x - a_f}}$$

$$= (p_f/c)^{k_2} \cdot {k_1}^{x - a_f - k_2}$$

If $k_2 \sim 0$ (i.e. $a_f = a_m \equiv a$), as has been the case in recent years, a satisfactory approximation is $R(x) = {k_1}^{x-a}$. The regression of log $R(x)$ on $(x - a)$ will then be linear with slope log k_1 (Fig. 10). This procedure yields $k_1 = 0.784$, and if we take the overall rate of survival to be 0.509, we obtain $p_f = 0.571$ and $p_m = 0.447$.

Population Dynamics

POPULATION PARAMETERS

From the data presented above, a life table for this population of whitefish can be constructed.

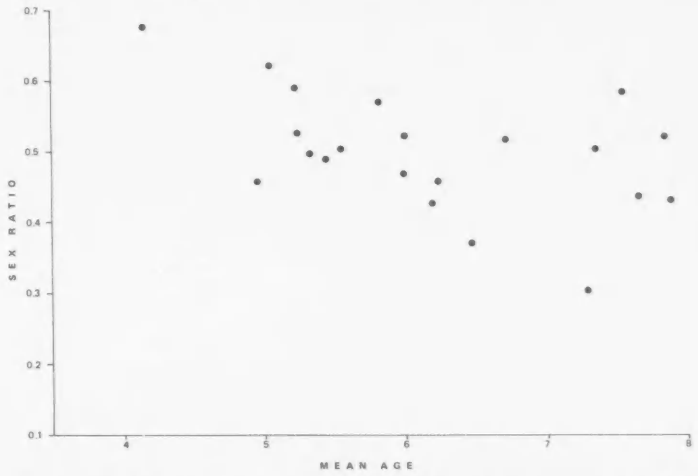

FIG. 9. Relationship between sex ratio (SR) and mean age (MA) of samples. The regression equation is: $SR = 0.736 - 0.038\ MA$, with $r = 0.487$, $0.01 < P < 0.05$.

TABLE 2. Sex ratio (SR) in different age-classes from years 1944–75. Sex ratio is fraction of males.

Age	*N*	SR ± 1 SE
3	229	0.672±0.059
4	1367	0.634±0.026
5	2027	0.548±0.022
6	1526	0.492±0.025
7	1083	0.425±0.030
8	469	0.409±0.045
9	190	0.326±0.067
10+	121	0.314±0.085

This can be used to solve the Lotka equation by iteration, yielding a value for the finite rate of increase of the population of 1.02 in 1975. This compares quite well with the value of 1.195 obtained empirically by comparing the test gang data for 1971 and 1975, as described above. The calculated mean generation period for the population was 8.62 yr.

The schedules of maturity and fecundity are to a very great extent determined by size independently of age (shown above). Moreover, it has been found that appropriate measures of size (length, weight, and condition) have declined markedly since 1941 (Handford et al. 1977). It follows that over the last 35 yr, there was probably a tendency for the whitefish to become less fecund and to mature later in life. Unless compensatory changes have occurred in processes for which there is no long-term data, e.g. in the rates of survival during the first few years of life, this will inevitably have reduced the intrinsic rate of natural increase of the population. Thus, the capacity of the whitefish population to resist exploitation has probably been steadily eroded since the 1940s.

The life history of the Lesser Slave whitefish may be compared with the data collated by Healey (1975; see also Healey and Nicol 1975; Bidgood 1974). He found the average rate of survival in unexploited populations to be about 0.51, which agrees well with our estimate of 0.53. His estimate of the average survival of whitefish in exploited populations is 0.36, however, which is lower than any of the averages computed for the Lesser Slave Lake population. This suggests that this population has been relatively lightly exploited, despite its collapse in the mid-1960s. At the same time, the Lesser Slave whitefish today have low fecundity and delayed maturation relative to other stocks, and this may have inhibited their capacity to respond to a given degree of exploitation. This argument in turn hinges on the abnormal secular trends in mean age and in growth-related parameters observed at Lesser Slave Lake, which are discussed by Handford et al. (1977).

OSCILLATIONS, LIMIT CYCLES, AND THE COLLAPSE

After an early period of high yield, the whitefish catch from Lesser Slave Lake declined steadily until about 1928 and then oscillated with rather large amplitude between 1928 and 1964, when

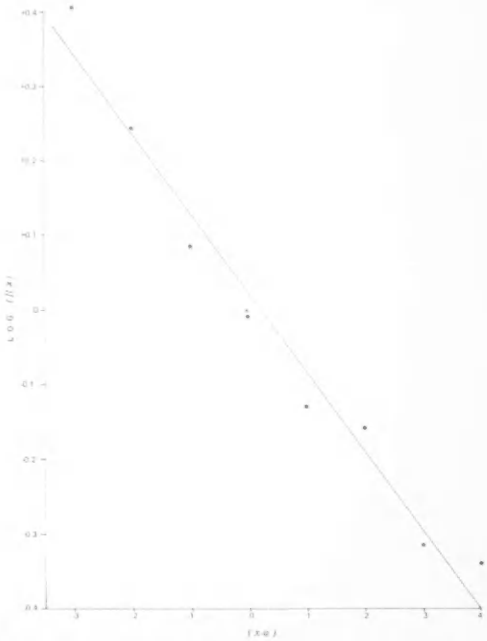

FIG. 10. Relationship between sex ratio and age, used to calculate the ratio of male to female survival rate. $R(x)$ is the ratio of males to females at age x, and a is the mean age at maturity. The equation of the regression is: $\log R(x) = 0.0247 - 0.1056\,(x - a)$, with $r^2 = 0.967$.

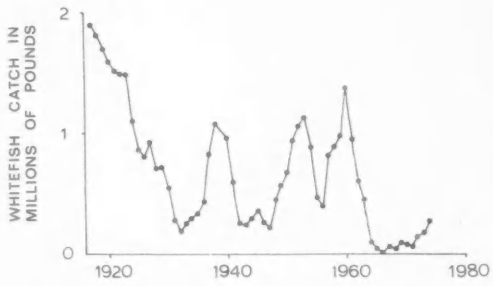

FIG. 11. Catch statistics for Lesser Slave Lake whitefish, 1917–74.

it collapsed and was closed until 1971: a slow recovery is now taking place (Fig. 11). This pattern of events — oscillations leading to collapse after a year of unusually high catch — is not uncommon in coregonid fisheries (Holling 1973). Two lines of evidence suggest that the collapse was not caused by chronic overfishing. The first, discussed above, is that rates of exploitation at Lesser Slave Lake do not appear to have been as great as in most other fisheries. The second is that the average catch from the lake over the last 30 yr has not been excessive, when compared with other Alberta fisheries. Fishery statistics for 10 or more consecutive yr are available for 48 Alberta lakes, excluding Lesser Slave Lake; these statistics (Table 3) comprise the mean whitefish catch (WFC), the latitude (LAT) and surface area (AREA) of the lake, the mean number of licenses issued for the lake (LIC), and the yardage (YARD) and mesh size (MESH) of the permitted gear. The multiple regression equation which relates these variables is:

$$\mathrm{WFC} = 31777.5 - 8905.2\mathrm{LAT} + 189.7\mathrm{AREA} + 97.2\mathrm{LIC} + 1664.6\mathrm{YARD} + 895.5\mathrm{MESH}$$

This regression has $r^2 = 0.828$, almost all of which is contributed by the first three independent variables. This descriptive equation can be extrapolated to predict the expected mean catch at Lesser Slave Lake, since the statistics for this lake were not used in the analysis. The prediction is 259380 kg, with an SE of 13143 kg; the observed mean catch from Lesser Slave Lake was 238961.5 kg. Prediction and observation are in good agreement, the probability that as large a deviation would have been caused by chance alone being about 0.12. These results may be interpreted to mean that the description of the 48 other Alberta lakes given by the multiple regression equation is also a good description of Lesser Slave Lake. However, in these other lakes considered together, the mean catch has not declined over the past 30 yr. Nor is this an artifact concealing the successive collapses of different lakes; all have fluctuated to some extent, of course, but only three collapsed. In short, the average catch from Lesser Slave Lake does not seem to be abnormally high, relative to that from other Alberta lakes, and this lends support to the notion that the whitefish stock has not been chronically overexploited.

Between about 1928 and 1964 the whitefish catch oscillates strongly. During the same period the number of fishermen also oscillates; the catch per fisherman, an index of whitefish abundance, therefore necessarily oscillates too (Fig. 12). There is a lagged relationship between the number of licenses issued and the catch per license (Fig. 13); the number of licenses issued increases to a peak 2 or 3 yr after a peak in the catch per license (Fig. 14). This analysis is restricted to the period 1940–64, but data presented by Miller (1941; unpublished report) indicate a similar relationship during 1930–40 (Fig. 15). We suggest that the observed fluctuations in the annual catch of whitefish reflect the existence of limit cycles in the whitefish

TABLE 3. Whitefish fishery statistics for 49 Alberta lakes, 1943–70. Lesser Slave Lake was not included in the stepwise regression analysis referred to in the text. DY: number of years for which data is available; WFC: mean whitefish catch (kilograms) per year; LAT: degrees north latitude above 50°N; AREA: surface area ($m^2 \times 10^6$); LIC: mean licenses issued per year; YARD: permitted yardage of gill nets (yards $\times 10^2$); MESH: permitted stretched measure of gill nets (inches).

LAKE	DY	WFC	LAT	AREA	LIC	YARD	MESH	
Amisk	26	317.5	4.58	5.26	13.9	6	4	1
Battle	16	12433.0	2.97	4.45	212.9	1	5.5	2
Beaver	28	19087.2	4.72	37.82	113.9	3	5.5	3
Bourque	22	4150.4	4.67	4.68	8.32	6	5.5	4
Buck	28	33955.9	2.98	31.16	510.4	2	5.5	5
Calling	13	12768.6	5.25	141.65	49.04	6	5.5	6
Christina	25	5461.25	5.63	38.85	7.20	6	5.5	7
Cold	22	78380.8	4.55	348.37	215.56	6	5.5	8
Elinor	27	3324.8	4.67	8.20	20.37	3	5.5	9
Ethel	17	1542.2	4.53	8.20	12.76	6	5.5	10
Fawcett	28	6372.9	5.32	31.16	27.71	6	5.5	11
Fork	14	12138.1	4.47	13.81	128.5	1	5.5	12
Frenchman	10	4250.2	4.53	9.93	36.44	5	5.5	13
Frog	19	18520.2	3.92	62.16	6.29	6	3.5	14
Graham	22	18470.3	6.58	43.28	12.14	6	5.5	15
Gregoire	10	1279.1	6.45	23.3	3.20	6	4	16
Heart	28	5225.4	5.03	32.12	29.5	6	5.5	17
Helena	24	4794.5	4.68	6.99	46.54	3	5.5	18
Iosegun	15	4957.8	4.47	13.38	44.67	3	5.5	19
Ironwood	23	3352.1	4.60	9.59	19.48	4	5.5	20
Island	16	3497.2	4.83	7.77	20.44	3	5.5	21
Lac La Biche	27	73273.3	4.83	222.75	285.6	3	5.5	22
Lac La Nonne	20	7888.0	3.93	13.36	90.75	3	5.5	23
Lac St Anne	27	31443.0	3.70	49.78	167.7	3	5.5	24
Lesser Slave	28	238961.5	5.42	1193.87	286.36	10	5.5	
McGregor	28	77187.8	0.42	40.47	121.93	3	5.5	25
Mistehae	11	54.4	5.93	9.28	3.09	6	4	26
Moose	28	9675.13	4.25	38.85	54.11	6	5.5	27
Muriel	28	36187.6	4.15	63.17	141.71	6	5.5	28
Newell	28	88064.9	0.43	71.23	128.07	4	5.5	29
North Buck	28	3628.7	4.68	15.54	35.43	3	5.5	30
N. Wabaska	15	22951.8	6.00	99.48	29.73	6	5.5	31
Orloff	28	2531.1	5.48	18.39	13.00	6	5.5	32
Peerless	23	15553.7	6.62	82.62	10.09	6	4.5	33
Pigeon	25	121181.7	3.02	103.60	474.96	3	5.5	34
Pinehurst	28	8491.3	4.65	36.42	70.32	6	5.5	35
Rock Island	27	5846.8	5.37	18.23	13.37	6	5.5	36
Round	16	3011.85	6.77	5.57	4.19	6	5.5	37
Sandy	26	4898.8	5.83	27.20	11.08	3	5.5	38
Skeleton	14	5125.6	4.62	18.13	54.21	3	5.5	39
Smoke	16	6019.2	4.37	9.96	32.94	3	5.5	40
S. Wabaska	10	916.3	5.92	50.59	24.90	6	4	41
Sturgeon	27	18542.9	5.10	40.47	25.52	2	5.5	42
Tucker	15	4.5	4.53	6.20	4	6	4	43
Utikuma	16	47427.6	5.83	275.58	96.00	6	5.5	44
Wabamun	24	114219.1	3.53	90.65	831.17	3	5.5	45
Whitefish	25	11602.9	4.73	31.51	88.96	6	5.5	46
Winefred	24	38813.9	5.50	111.82	21.33	6	5.5	47
Wolf	25	7946.9	4.70	30.43	28.68	6	5.5	48

population, driven by the lagged response of a predator population (the fishermen) to changes in the abundance of its prey (the whitefish).

It has not been possible to rule out the converse hypothesis, that it is the whitefish stock which is responding in a lagged manner to changes in the abundance of fishermen. This will make no difference to our interpretation of the dynamics of the system. However, we prefer the former interpretation, because conversations with fisher-

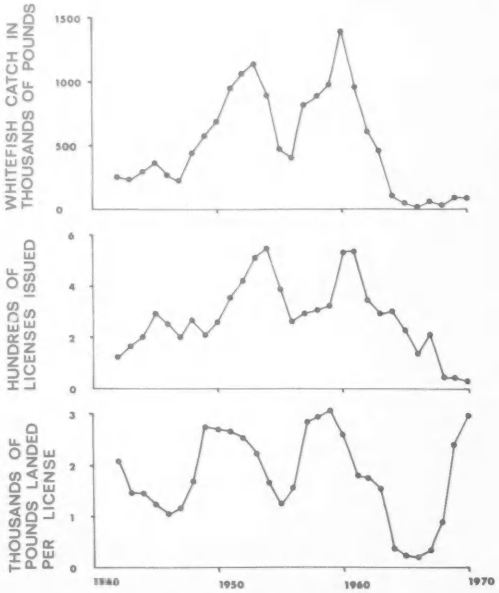

FIG. 12. Fluctuations in whitefish catch, number of licenses and catch per license for Lesser Slave Lake.

men at Lesser Slave Lake have confirmed that the recent history of the fishery is an important element in making a decision whether or not to fish the lake in a given year, a decision that may involve a considerable expenditure of money and time. This has been seen particularly clearly since the reopening of the fishery in 1971. At first, fewer than 40 men were willing to take the risk of fishing the lake, but after two difficult seasons, they obtained very high catches per individual in 1973 and 1974. By 1975 the news had spread, and more than 300 licenses were taken out.

If this hypothesis is true, the collapse of the fishery might be explained in one of two ways. First, the system might be inherently unstable, the oscillations tending to increase in amplitude until the population becomes extinct or reaches some critical threshold below which recovery is not possible. Secondly, stochastic deviation from the expected population number might expose the population to serious risk of extinction when it occupies a trough in the cycle, whether the cycle is deterministically stable or not. Moreover, the driving parameters of the system (e.g. the intrinsic rate of increase, and therefore the natural period, of the population), have changed in time and this could shift the system from one type of behavior to another (May 1973; Holling 1973). Certainly, if the capacity of the whitefish to respond numerically to exploitation has been eroded in recent years, it seems intuitively likely that this would prejudice its recovery from very

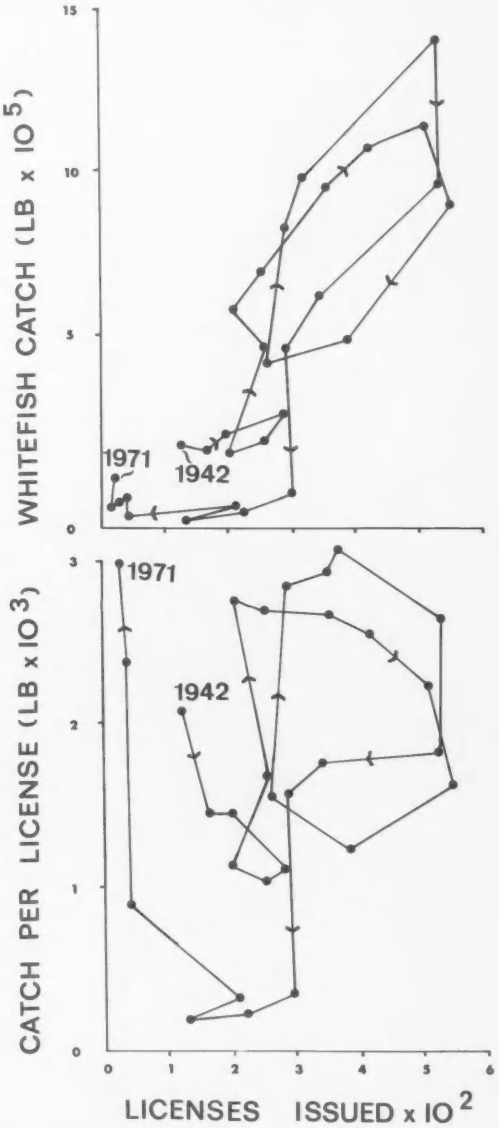

FIG. 13. Diagrammatic representation of predator–prey cycles in the Lesser Slave Lake fishery. a, Whitefish catch versus number of licenses; b, whitefish catch per license vs. number of licenses.

low population levels, especially given the rather large short-term fluctuations in life history variables often noticed in whitefish populations (e.g. Nikolskii 1969; Aass 1972; Davidoff et al. 1973). The data available from Lesser Slave Lake, although very extensive, are insufficient to enable us to distinguish rigorously between the different possible types of behavior that might be exhibited

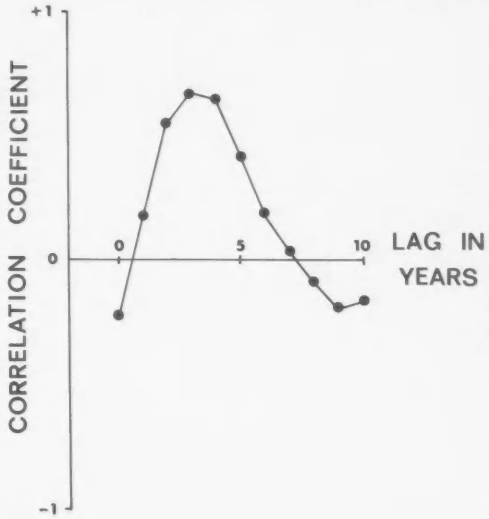

FIG. 14. Crosscorrelegram of catch per license vs. number of licenses.

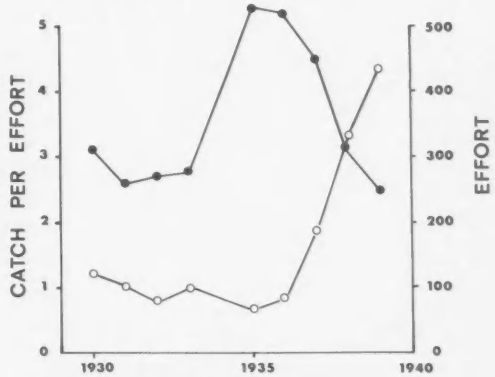

FIG. 15. Relationship between catch per unit effort and effort in the 1930s. Redrawn from figure in unpublished report of R. B. Miller. "Effort" is described by Miller as "men X nets"; catch per effort is in thousands of pounds of whitefish. ●, catch per effort; ○, effort.

by a two-species predator–prey system. We therefore take the conservative view that the observed oscillations represent a deterministically stable limit cycle and that the collapse was caused by stochastic events during a trough in this cycle. It is ironic that, although the prevailing philosophy of management is to attempt to harvest the maximum sustainable yield from a stationary population, it has been management policy that appears to have been responsible for the destabilization of the Lesser Slave whitefish stock, through the laissez-faire issue of licenses. Other common management practices may also contribute to this dangerous situation. For example, to raise the permitted catch when the catch in the preceding year has shown an increase will act as a potent destabilizing influence.

If this interpretation is accepted, the biological solution to the problem of extreme fluctuations in whitefish yield is clear. The issue of licenses should be restricted to a constant number per year, preferably granted to a small number of professional fishermen who live by the lake and in whose interest it will be to fish within the limit and to report catches accurately. The limit itself should be held constant and should not be varied in an attempt to accommodate the inevitable stochastic fluctuations in yield. Finally, the price paid to the fishermen should also be held constant to avoid an erosion of their economic base and thus a demand for an increase in the permitted catch. The radical nature of these proposals emphasizes the need for a critical review of the effect of management policies on the dynamics of whitefish populations, which is, however, outside the scope of the present paper.

Acknowledgments

J. Weisgerber and D. Rubyiak obtained the raw data on fecundity. We thank Dr M. C. Healey for a thorough and useful review of an earlier version of this manuscript.

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A Gillnet Fishery Considered as an Experiment in Artificial Selection

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HANDFORD, P., G. BELL, AND T. REIMCHEN. 1977. A gillnet fishery considered as an experiment in artificial selection. J. Fish. Res. Board Can. 34: 954–961.

Temporal patterns of change in growth, condition, and mean age of samples of lake whitefish (*Coregonus clupeaformis*) taken from Lesser Slave Lake, Alberta, during 1941–75 are described. Growth rate and condition have declined, while mean age has increased. Gillnet fisheries are highly selective of large, heavy, fast-growing individuals, and we suggest that culling of this sort will provoke an evolutionary response in the stock, which may be reflected in patterns of change in growth and age. This hypothesis and others are discussed, and the general importance of artificial selection in lake fisheries is briefly considered. The possible implications for fishery management are outlined.

Key words: artificial selection, evolution, growth rate, gillnet, *Coregonus clupeaformis*.

HANDFORD, P., G. BELL, AND T. REIMCHEN. 1977. A gillnet fishery considered as an experiment in artificial selection. J. Fish. Res. Board Can. 34: 954–961.

Nous décrivons les changements qui se sont produits avec le temps dans la croissance, l'état d'embonpoint et l'âge moyen d'échantillons de grands corégones, *Coregonus clupeaformis*, prélevés dans le Petit lac des Esclaves, Alberta, durant 1941–75. Le rythme de croissance et l'état d'embonpoint ont diminué, alors que l'âge moyen a augmenté. Les pêches au filet maillant sont hautement sélectives en faveur d'individus grands, lourds et à croissance rapide, et nous croyons qu'une sélection de cette nature déclenchera une réponse évolutionnaire dans le stock, qui pourrait se refléter dans des changements dans la croissance et l'âge. Nous analysons cette hypothèse ainsi que d'autres, et discutions brièvement de l'importance de la sélection artificielle dans les pêches lacustres. Nous esquissons les implications possibles pour la gestion des pêches.

Received April 5, 1976
Accepted March 10, 1977

Reçu le 5 avril 1976
Accepté le 10 mars 1977

WHEN the rate of mortality in a population of fish is increased by exploitation, competition for food may be reduced, causing an increase in individual growth rates. At the same time, the removal of the older (and larger) fish increases the representation of younger animals in the population, leading to a decrease in mean age. This effect of exploitation on mean age and growth rate has often been observed in populations of whitefish, and indeed Healey (1975) has used it as a criterion of the ability of a fish stock to withstand further exploitation.

We have analyzed data from experimental and commercial catches of lake whitefish (*Coregonus clupeaformis*) from Lesser Slave Lake, central Alberta, between 1941 and 1975 and have found that in several respects they do not conform to the scheme outlined above. In this paper we describe the relevant features of the data, and offer an explanation of them in terms of an evolutionary response to the selective effects of exploitation by a gillnet fishery.

Materials and Methods

Lesser Slave Lake is a mesotrophic lake about 1200 km^2 in extent that has been fished commercially since the turn of the century. Lake trout (*Salvelinus namaycush*) was fished out by the 1920s and is now extinct; the other commercial species, walleye (*Stizostedion vitreum vitreum*), cisco, or tullibee (*Coregonus artedii*), and lake whitefish, have all shown progressive declines in abundance (Alberta Fish and Wildlife unpublished data). In 1965 the whitefish fishery collapsed and was closed until 1972; in 1971 the cisco fishery collapsed and is still closed.

Most of the samples discussed here are from the commercial catch, but some were obtained from test nets set from 1965 onwards. Only catches from the 5 and 5½-in. meshes have been used in the present analysis. From the records for each sample, we have the weight and length of all individuals in the sample; we have restricted the analysis to males to avoid any complications caused by the sampling of gravid

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Printed in Canada (J4278)
Imprimé au Canada (J4278)

females, but the data for females have been analyzed and are in no way substantially different. Ages were determined as described by Bell et al. (1977). From these data we have calculated the secular changes in length and weight at given age, in mean age, and in condition. The condition factor, k, is computed as $10^5\ W/L^3$, where W is wet weight in grams and L is fork length in millimetres; it is thus a measure of the fatness of the fish.

Results

All year-classes show an initial increase in mean weight between about 1941 and 1945, this increase being most marked in the older fish. Thereafter, despite some fluctuation, all classes show a progressive decline. This decline was steeper in older fish, so that at present there is much less difference between young and old fish than there was 30 yr ago; fish of given age now weigh less than half of what they did in the mid-1940s (Fig. 1). Fork length has changed over the years in a way similar to weight (Fig. 2). In contrast with weight, however, the decline in length did not begin until about 1958 and has been such that mean length at given age is now approximately the same as in the early 1940s. As with weight, there is at present much less difference between young and old fish than there was formerly. Condition has declined dramatically in all age-groups since 1941; the curve is steepest during the 1950s and is now apparently almost asymptotic (Fig. 3). This decline is not an artifact of month of capture, which does not vary systematically from year to year and which could only produce changes of much small magnitude in any case. Again, although condition is related to mean length, it varies within a given year by only about 0.25 units of k over the extreme length range of 34–54 cm; moreover, condition declines with increasing length, while the opposite relationship would be required to contribute to the situation shown in Fig. 3.

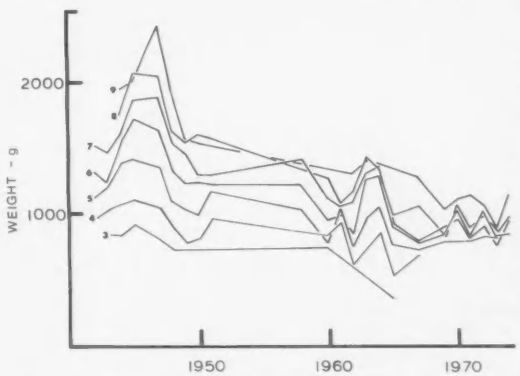

FIG. 1. Changes in weight at given age in samples of lake whitefish (*Coregonus clupeaformis*) from Lesser Slave Lake, 1940–75.

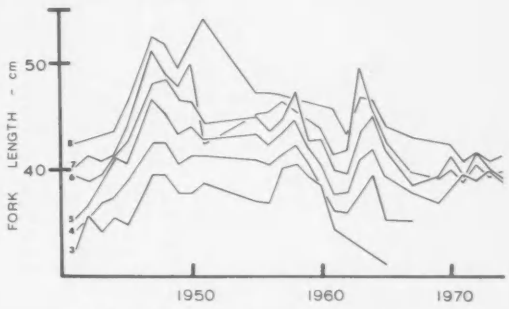

FIG. 2. Changes in length at given age in samples of lake whitefish from Lesser Slave Lake, 1940–75.

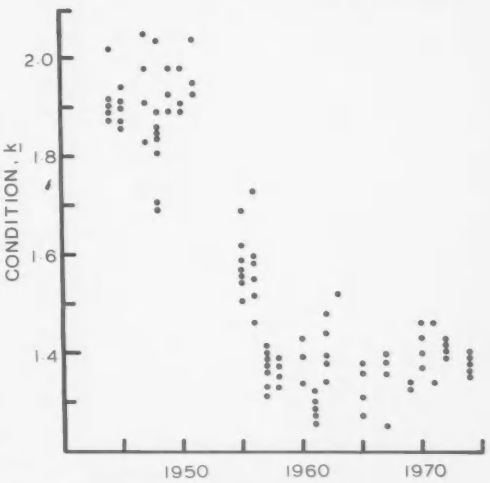

FIG. 3. Change in condition ($k = 10^5 W/L^3$) of male lake whitefish from Lesser Slave Lake, 1940–75.

Finally, under continued exploitation catches have shown an overall increase in mean age, although with temporary periods of decrease in the early 1940s and the mid-1950s (Fig. 4). It is evident that this progression from a mean age of 4–5 yr to one of 7–8 yr is not a simple consequence of the precession of strong year-classes, although of course these do occur and may be traced through the data (Table 1).

Selective Netting Hypothesis

Gill nets select a narrow range of fish from the fish stock, with regard to overall size and body proportions (see extensive review in Hamley 1975), yet the possibility of an evolutionary

TABLE 1. Age composition (expressed as percent of catch) of commercial catches of lake whitefish (*Coregonus clupeaformis*), Lesser Slave Lake, Alberta, 1941–74.

			Age (yr)										
		n	2	3	4	5	6	7	8	9	10	11	12
	1941	109	3.7	2.8	9.2	27.5	24.8	17.4	12.8	0.9	0.9	—	—
Oct.	1942	48	—	2.1	6.3	33.3	50.0	8.3	—	—	—	—	—
Feb./June	1943	161	—	14.9	32.9	27.3	18.0	5.0	1.2	0.6	—	—	—
Sept.	1944	485	—	10.5	41.9	22.1	8.0	7.0	7.8	1.6	1.0	—	—
Oct.	1945	500	—	0.4	20.8	37.2	24.2	12.0	4.4	0.4	0.6	—	—
Oct./Nov.	1947	601	0.2	23.1	59.1	8.2	3.8	2.3	1.5	1.2	0.3	0.3	—
Sept./Oct.	1948	499	—	0.8	52.7	24.2	8.6	2.8	4.0	3.2	2.2	1.2	0.2
Aug./Sept.	1949	498	—	—	5.8	70.5	18.7	1.2	1.6	1.0	1.0	—	0.2
Aug.	1950	500	—	—	9.0	69.6	16.4	2.6	1.0	0.6	0.6	0.2	—
Aug./Sept.	1951	500	—	—	1.6	23.4	49.8	23.2	1.8	0.2	—	—	—
	1952	500	—	—	—	11.0	40.0	36.0	12.0	0.4	0.6	—	—
	1953	500	—	—	1.4	2.8	28.1	47.9	17.1	2.6	—	—	—
	1954	500	—	0.4	2.4	5.0	14.0	30.2	32.2	11.4	4.0	—	—
	1955	300	—	5.5	29.0	13.4	13.5	21.7	13.0	3.8	—	—	—
	1956	300	—	6.8	47.8	25.4	7.4	4.1	5.3	2.0	0.3	0.9	—
	1957	300	—	0.4	51.2	27.5	12.7	1.6	1.4	3.2	1.0	—	—
Sept./Oct.	1958	295	—	1.4	35.9	42.7	12.2	4.7	0.3	0.7	0.3	1.0	0.7
Sept./Oct.	1960	245	—	1.2	3.3	18.0	51.8	21.2	2.9	0.8	0.4	0.4	—
Sept./Oct.	1961	198	—	0.5	20.7	15.7	32.3	19.2	10.1	1.5	—	—	—
June	1962	201	—	—	5.5	21.9	18.4	23.4	22.9	7.0	1.0	—	—
July	1963	585	—	—	5.8	18.8	28.2	31.1	15.8	—	—	—	—
July	1964	69	—	—	8.7	8.7	13.0	23.2	15.9	23.2	4.4	2.9	—
Nov.	1965	17	—	—	5.9	29.4	41.2	5.9	17.6	—	—	—	—
	1967	33	—	3.0	6.1	24.2	30.3	12.1	6.1	6.1	9.1	—	3.0
	1969	46	—	—	2.2	8.7	39.1	34.8	4.3	6.5	—	—	4.3
Sept.	1970	82	—	—	1.2	1.2	12.2	31.7	29.3	15.9	7.3	1.2	—
Sept.	1971	50	—	—	—	4.0	16.0	32.0	20.0	24.0	4.0	—	—
	1972	65	—	—	—	4.6	13.8	12.3	38.5	20.0	9.2	1.5	—
June	1973	62	—	—	—	3.2	24.2	32.3	17.7	19.4	1.6	1.6	—
Oct.	1974	417	—	—	—	1.9	13.7	27.8	44.4	7.2	4.8	0.2	—
Aug.	1975	189	—	—	—	13.2	19.5	32.2	13.2	2.0	0.5	—	—

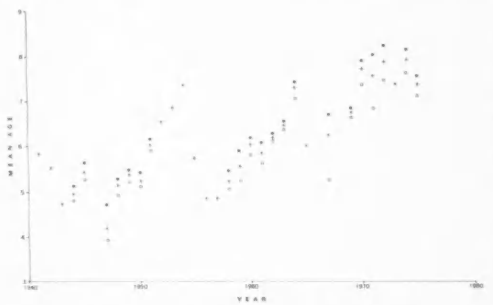

FIG. 4. Mean age of samples of lake whitefish from Lesser Slave Lake, 1940–75. ○, Males; ● females; and +, total catch.

response by culled populations has seldom been seriously considered (but see Miller 1957; Calaprice 1969; Schaffer and Elson 1975). In the following sections we raise and discuss this possibility.

The 5½-in. gill nets used in Lesser Slave Lake will selectively cull large fish with relatively large girth, i.e. high condition, which will be the fastest growing fish of a given age. Recent test-gang samples provide evidence for the contemporary selectivity of the gear used. Figure 5 is a scatter diagram of log weight and condition of male lake whitefish from a single large test-gang sample. The envelopes contain all individuals caught in a mesh of specified size. The selectivity of the 5–5½-in. gear for high weight and condition is readily apparent. Further, we have compared 5½-in. gillnet catches with trawl catches, which provide a more random sample of the available fish with respect to size and shape. In all cases, the fish in the gillnet samples have higher mean condition than those in the trawl samples (Table 2); the two-tailed probability of obtaining this result if there were really no difference between the two sampling techniques is about 10^{-5}. In 14 of a total of 16 comparisons of the coefficient of variation of condition between the gillnet and

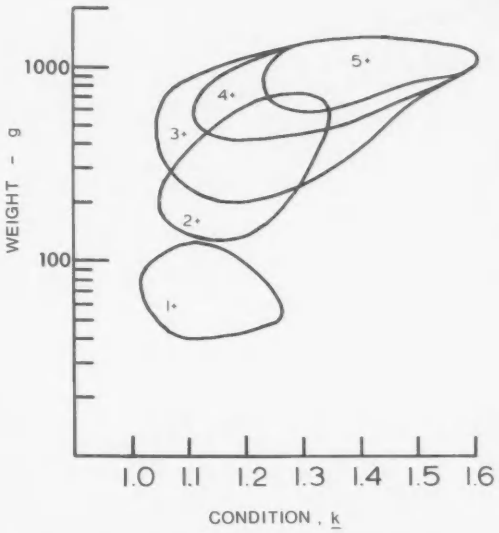

FIG. 5. Scatter diagram of weight and condition, k, of a test-net sample of male lake whitefish, August 1975. Envelopes contain all individuals caught in mesh of indicated size.

TABLE 2. Mean condition of male whitefish in various samples taken in 1974 from Lesser Slave Lake.

	Age (yr)							
	2	3	4	5	6	7	8	9
Trawl								
1	1.21	1.20	1.22	1.24	1.33			
2		1.18	1.23	1.28	1.30	1.29	1.31	
Gill net								
1				1.39	1.38	1.39	1.36	
2					1.34	1.41	1.38	
3				1.41	1.38	1.32	1.35	1.26

trawl samples, the gillnet samples were less variable (Table 3); here, the one-tailed prediction (that the gillnet catches should be less variable) is significant beyond the 1% level. We can therefore conclude that the mortality caused by 5½-in. gill nets acts to reduce mean condition and phenotypic variation of condition.

There has been a decline in the coefficient of variation of condition with time (Fig. 6, which has $r = 0.447$, $P << 0.01$). This decline is shown by all age-groups and so cannot be an artifact of the increasing mean age of the samples. Reduction of the variance of condition is of course much steeper than the reduction of the coefficient of variation because of the trend towards lower mean values of condition in time. We have also found that mean condition declines with age within a cohort and that the rate of change in

TABLE 3. Coefficient of variation of condition of male whitefish in various samples taken in 1974 from Lesser Slave Lake.

	Age (yr)							
	2	3	4	5	6	7	8	9
Trawl								
1	4.60	5.60	6.19	4.34	8.29			
2		7.40	6.02	8.12	7.83	8.55	8.31	
Gill net								
1				5.53	3.43	6.53	4.85	
2					7.55	6.67	4.62	
3				3.34	8.15	7.49	3.69	2.56

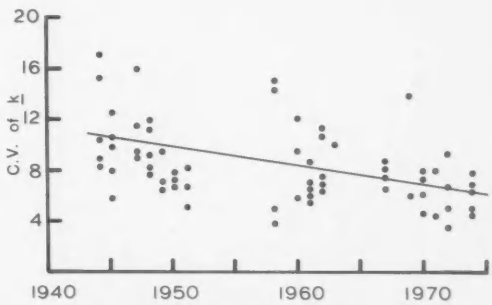

FIG. 6. Change in coefficient of variation of condition (C.V. of k) with time of male lake whitefish.

condition with age within a cohort diminishes in time.

Evidence that growth rate and characters related to the growth rate are to some degree inherited comes from response-to-selection experiments and from the direct estimation of heritability by inbreeding techniques. The recent literature includes work by Lewis (1944); Alm (1949); Donaldson and Olson (1957); Moav et al. (1964, 1974); Moav and Wohlfarth (1968); Calaprice (1969, 1970, 1974, 1976); Gall (1969); Donaldson (1970); Ryman (1970, 1971); Aulstad et al. (1972); Lindroth (1972); Kincaid (1972); Ricker (1972); Millenbach (1972); Naevdal et al. (1975); Gjedrem (1975, 1976); and Gunnes and Gjedrem (1976). In general, it is clear that growth rates will usually respond fairly quickly to selection, and we feel that the statement by Gjedrem (1976) that "the few estimates [of heritability] for growth-rate are moderately large ($h^2 = 0.1$–0.2)" is, if anything, conservative.

Fishing mortality, although not as great as in many other lakes, constitutes a significant proportion of the total mortality of the catchable fish stock at Lesser Slave Lake (see Bell et al. 1977). Moreover, this mortality is distinctly nonrandom with respect to condition and overall size, and therefore also with respect to age and growth

rate. Since these characters have moderately large heritabilities, the selective mortality represented by fishing is likely to permanently change the genetic composition of the stock. In other words, gillnet fisheries represent enormous experiments in artificial selection and will probably cause evolutionary change. This verbal argument suffices to establish our case, and all the phenomena described in the previous section are consistent with such a hypothesis; there have been declines in weight and length at given age, more marked in the case of weight, and a consequent decline in mean condition. Even more significantly, we have demonstrated the decline in the phenotypic variance of condition that is to be expected if selection is acting. Unfortunately, it is impossible to construct a convincing quantitative argument because of the lack of trawl data before 1974. Over the 30 yr of the study, condition has declined by about 0.6 units of k, or by very roughly 0.1 units per generation. The rate of advance under selection is defined to be the product of the applied selection differential (that is, the difference in the mean of the character studied between the population at large and the selected parents) and the heritability. Selected (gillnet) and unselected (trawl) samples differed in 1974 by about 0.11 units of k (data of Table 1), and on average about 30% of the total mortality is caused by fishing (Bell et al. 1977). For heritabilities of between 0.1 and 0.5, the rate of change in k under selection cannot be much more than 0.01 units per generation, which is consistent with our observation that the rate of change is at present very slow (Fig. 3). However, this does not shed much light on events during the critical period of the 1950s. The phenotypic variance of the population was then much greater, and we would expect the selection differential to be correspondingly greater; we would also expect heritability to be greater, because at this time the additive genetic variance of growth-related characters had not yet been depleted by selection. A very simple assumption would be that the phenotypic variance and the selection differential were directly related, in which case we should expect an initial response to selection of 0.05–0.08 units of k per generation, which is about half the change that we observe. This is pushing the data to the limit, however, and the fact that the selection differential and the heritability will have varied in time, in such a way that the direction of change can be stated but the rate of change cannot, vitiates any attempt to obtain more precise predictions. However, there is clearly no obstacle in principle to the idea that the observed changes were caused primarily by selection.

Selection will produce individuals, which by being smaller, will live longer before reaching cullable size and will therefore act to increase the rate of survival of adult fish, relative to a population that did not respond in this way. Consequently, the mean age at maturity will increase, and the age-specific fecundity will be diminished, insofar as these are determined by size rather than by age. These effects will combine to raise the mean age of the population, and at moderate fishing intensities this effect may be sufficiently powerful to reverse the expected trend towards a younger age-distribution. This is what appears to be happening in Fig. 4. This phenomenon is only to be expected in an intermediate range of fishing intensities. In a very lightly fished population, the selection differential will be too slight to provide an effective force, while in heavily exploited populations the selective effect will be overpowered by the usual demographic shift towards younger age-groups caused by density-dependent effects on individual growth.

Discussion

We have examined other interpretations of the data. Activities associated with oil exploration have greatly increased siltation in part of the lake's drainage basin (Wyldman and Poliguin 1972). Excessive siltation may reduce egg hatching success, and, since whitefish are visual feeders, may also reduce feeding success and thereby inhibit growth; growth may also be deleteriously affected by the effect of siltation on the abundance of food organisms. However, the growth-related changes described above were well underway before the period of serious oil exploration began in 1957–60 (Mudroch unpublished data). Further, it is not clear why siltation, if it depressed the growth-rate, should also produce a decline in the variance of condition. Siltation apart, there is no reason to believe that the pertinent features of the lake have changed greatly over the period in question; there has been little or no accumulation of nutrients from local farms or communities, and the water quality has been described in a recent report as "pristine."

In other lakes, increases in the mean age of fish stocks have been interpreted as being simply reflections of changes in the strengths of individual year-classes (e.g. Christie 1963; Lawler 1965). This is quite convincing for short periods of time, but for long periods of directional change in mean age it ceases to be satisfactory. However, the passage of a number of strong year-classes can be traced through the data (Table 1, Fig. 4).

Returning to the selective netting hypothesis, we shall briefly consider its generality as a significant factor in determining the qualitative response of an exploited fish stock, although it is not our intention to present a review. It is a commonplace that many exploited stocks of fish now provide smaller fish; however, little long-term data on growth and age in other whitefish populations are available in the published literature. There is suggestive but inconclusive data from two other Alberta fisheries. At Sturgeon Lake, a small lake to the west of Lesser Slave Lake, the whitefish have declined in condition and in weight at given age between 1969 and 1974 (Bishop personal communication; Table 4 and 5); this lake has supported a 6¼-in. gillnet fishery since the 1920s. However, there appears to be no information available on other changes in the lake during this period, so the data must be treated with reserve. Bidgood (1973) has described a decline in the growth rate of the Pigeon Lake, Alberta, stock between 1956 and 1970. He has attributed this trend to changes in food availability, interspecific competition for food, and increased intraspecific competition for food following a supposed proliferation of the whitefish caused by a reduction of the pike population. It is not clear from his data to what extent this situation is comparable to Lesser Slave Lake, but we may note that the Pigeon Lake stock has been subject to a fishery that has twice reduced its permitted mesh size, from 140 mm to a final 89 mm. Increased intraspecific competition can hardly be relevant to the situation at Lesser Slave Lake, where there has been no proliferation of the whitefish, rather the contrary, and where pike are still common. Nor do we find the hypothesis of interspecific competition very attractive. A recent survey of the diets of *Coregonus* and *Catastomus* in Lesser Slave Lake (Weisgerber personal communication and unpublished data; data available from Alberta Fish and Wildlife) has shown that, although the two forms feed on organisms belonging to the same or to similar families, there is very little dietary overlap at the species level; since the two forms have very different morphologies and ways of life, this result is not surprising. Finally, the most complete sequence of data on age composition is that available for the Lake Winnipeg stock, where Davidoff et al. (1973) show that mean age has decreased steadily since 1946. However, it is quite clear from Kennedy's (1954) paper that during the 9 yr prior to this there had been a consistent increase in mean age. Pending a thorough review of the literature, all that can be said is that declines in growth and condition appear to be quite common, but that the situation in Lesser Slave Lake may reflect an unusual set of circumstances. In the remainder of this discussion, we shall examine the effect of size-selective mortality on the fishery.

TABLE 4. Average weights (grams) of commercial whitefish caught in 6¼-in nets, Sturgeon Lake, Alberta, 1969–74.

Age class	1969 $n=72$	1970 $n=40$	1971 $n=38$	1972 $n=50$	1973 $n=100$	1974 $n=50$
I	—	—	—	—	—	—
II	—	—	—	—	—	—
III	—	—	700	—	—	—
IV	—	—	1295	926	—	—
V	1565	1460	1400	1125	1078	—
VI	1831	1596	1610	1528	1204	1145
VII	2068	1940	1875	1703	1517	1234
VIII	2114	2325	1823	1800	1654	1780
IX	2498	2310	2113	1784	1803	1630
X	2661	2482	2424	1935	1980	—
XI	2779	2660	2566	2365	1957	—
XII	—	3140	2790	2445	1773	2040
XIII	—	—	—	2170	1720	—
XIV	—	—	—	—	2220	—

TABLE 5. Condition factors (k) of commercial whitefish caught in 6¼-in nets, Sturgeon Lake, 1969–74.

Age class	1969 $n=72$	1970 $n=40$	1971 $n=38$	1972 $n=50$	1973 $n=100$	1974 $n=50$
IV	—	—	1.53	1.39	—	—
V	1.67	1.41	1.52	1.35	1.45	—
VI	1.58	1.48	1.25	1.33	1.54	1.43
VII	1.55	1.45	1.41	1.32	1.35	1.37
VIII	1.47	1.63	1.31	1.35	1.38	1.56
IX	1.52	1.46	1.31	1.18	1.27	1.21
X	1.45	1.37	1.40	1.24	1.33	—
XI	1.47	1.38	1.39	1.29	1.35	—
XII	—	1.49	1.43	1.25	1.18	1.13
XIII	—	—	—	1.17	1.10	—
XIV	—	—	—	—	—	—
IV	—	—	—	—	—	—
$\bar{k}$	1.49	1.46	1.39	1.28	1.31	1.34

The life-history parameters of any unexploited stock of fish must be such that the population is able in the long term to maintain a rate of increase of zero. Exploitation implies a change in certain of these parameters; notably, the rate of survival of adult fish will be reduced. These changes will tend to reduce the rate of increase of the population, which, other things being equal, will become extinct. Only if other life-history parameters vary in such a way as to counterbalance the reduction of adult survival can the population persist. Only one such mechanism appears to be recognized in the current Western literature: this is the existence of certain density-dependent constraints on population growth. These might operate, for example,

if competition for food were reduced at some or all ages because of the reduction of population density. This would increase the rate of growth of fish beyond the age at which the effect occurred, and in this section of the population individuals of any given age would be larger than individuals of the same age in an unexploited population. To the extent that demographic schedules are dependent on size rather than on age, this will tend to increase fecundity and to decrease the age at maturity; there may also be a reduction in the mortality of very young fish. At the same time, an increase in the rate of growth will reduce the age at which individuals are recruited into the exploited section of the population, and will therefore increase the mortality experienced by at least some age-classes. Clearly, the overall effect of exploitation on the rate of increase of the population will depend on the relative magnitudes of its beneficial effect on fecundity, maturation, and early survival, and its deleterious effect on the survival of juvenile and adult fish.

This, the conventional account of the response of fish populations to exploitation, is incomplete in one important respect; it assumes that the population comprises uniform individuals whose inherited characteristics do not change with time. This is quite unlikely to be true. In a gillnet fishery, for example, only fish of greater than given dimensions are fully exposed to the risk of capture. Thus, it is inevitable that, over a certain range of age-classes, the largest individuals of given age will be selectively removed from the population. This will lead to the evolution of a slower rate of growth, that is, to smaller size at given age. Since this implies lower fecundity and delayed maturity, size-specific selection will probably reduce the rate of increase of the population and will thus diminish its ability to respond to further exploitation. Selection will, of course, always tend to maximize the rate of increase of a population; in this case, however, it is maximized relative to a population which, undergoing the same rate of exploitation, did not respond by evolving a slower rate of individual growth. But the selected population, if it were abruptly released from exploitation, would display a lower rate of increase than the original population before exploitation. Thus, density-dependent compensation and size-specific selection act in opposite senses, the former acting to increase the individual growth rate and the rate of population increase, and the latter, vice versa.

This argument requires that the schedules of maturity and fecundity be determined to some extent by age as well as by size. To prove this, imagine the fishery to be so efficient that, once an individual should exceed a certain size, it is immediately captured. But an individual with high growth rate will mature earlier in life than a slow-growing individual, and, if fecundities at given size are equal, will usually have higher fitness because of its shorter generation period; indeed, the slow-growing individual will be at even more of a disadvantage than this argument suggests, since, maturing later in life, it will suffer more natural mortality. On the other hand, if demographic schedules are entirely age specific, then the only component of fitness affected by exploitation will be the rate of survival, and slow-growing individuals will always be the more fit. Thus, when the contribution of age, independently of size, to the schedules of fecundity and maturation exceeds some critical value, the selective removal of the larger fish of given age will favor the evolution of a slower rate of growth.

But if age makes a substantial contribution to the determination of fecundity and maturation, selection may act on the age-specific schedules as well as on the size-specific schedules; moreover, it will do so in fisheries (for example, trawl, longline, or seine fisheries) where selection for size may be negligible. For example, one possible response to the increase in mortality caused by exploitation might clearly be the evolution of a lower age at first reproduction, irrespective of the size at first reproduction. This has happened in some exploited stocks of whitefish (Healey 1975). Age-specific selection will again raise the rate of increase relative to that of an unexploited population that did not undergo selection, but it is also in principle capable of creating a rate of increase greater than that of the original unexploited population. Thus, it may act in concert with density-dependent compensation.

We conclude that present management theory may be seriously deficient in that it fails to take into account the possibility of adaptive genetic change in exploited stocks of fish. This is especially serious because the size-specific selection associated particularly with gillnet fisheries is capable of actually reducing the capacity of the population to maintain itself in the face of continued exploitation. Selection of this sort may only rarely be capable of determining the direction of change in population parameters, that is, that selection is only rarely capable of producing an effect larger than and opposed to that associated with density-dependent compensation. But even if this is so, selection would invariably enter into the dynamics of an exploited popula-

tion by influencing the rates at which population parameters change and the final extent to which they change. Until a synthetic theory appears in which ecological and evolutionary forces are recognized, it is unlikely that the behaviour of fish populations under exploitation can be fully understood.

Acknowledgments

We are grateful to Dr M. C. Healey for his critical reading of an earlier draft.

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Crustacean Zooplankton Communities as Indicators of Limnological Conditions: An Approach Using Principal Component Analysis

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SPRULES, W. G. 1977. Crustacean zooplankton communities as indicators of limnological conditions: an approach using principal component analysis. J. Fish. Res. Board Can. 34: 962–975.

Principal component analysis is used to develop a technique for predicting the limnological characteristics of a lake from knowledge of its midsummer limnetic crustacean zooplankton community. Patterns of variation in zooplankton community structure are summarized in the principal components extracted, via the species covariance matrix, from the matrix of transformed proportionate numerical abundances of species in a sample of lakes. The relation between these patterns and the limnological characteristics of the lakes is determined from the first-order rank correlations of the limnological variables with the components. In relatively undisturbed lakes of northwestern Ontario, results indicate that lakes characterized by *Cyclops bicuspidatus thomasi, Diaptomus minutus*, and others are large and clear, whereas those characterized by *Tropocyclops prasinus mexicanus, D. oregonensis*, and others are smaller and of lower water clarity. These patterns are contrasted with those extracted from the same data using more subjective techniques. In the acid-stressed Killarney region, Ontario, lakes dominated by *D. minutus* are predicted to be acidic, small, and clear, whereas those dominated by *Diaphanosoma leuchtenbergianum, Bosmina longirostris, Mesocyclops edax*, and others will be less clear, larger, and with higher pH. In Haliburton lakes, Ontario, those with *Diaptomus oregonensis, M. edax*, and *Ceriodaphnia lacustris* are predicted to be small and productive, whereas those with *D. minutus, D. sicilis, B. longirostris*, and *Daphnia dubia* will be larger and less productive. The usefulness of the technique and some modifications are discussed.

Key words: zooplankton communities, principal component analysis, ELA lakes, Haliburton lakes, Killarney lakes

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Utilisant l'analyse par constituants principaux, nous avons mis au point une méthode permettant de prédire les caractéristiques limnologiques d'un lac à partir de la connaissance de sa communauté de crustacés zooplanctoniques limnétiques à la mi-été. Nous résumons les schémas de variation dans la structure de la communauté zooplanctonique dans les principaux constituants extraits, via la matrice de covariance des espèces, à partir de la matrice d'abondance numérique proportionnelle transformée des espèces dans un échantillon de lacs. Nous établissons la relation entre ces schémas et les caractéristiques limnologiques des lacs à partir des corrélations des rangs de premier ordre des variables limnologiques avec les constituants. Dans des lacs relativement non dérangés du nord-ouest de l'Ontario, les résultats indiquent que les lacs caractérisés par *Cyclops bicuspidatus thomasi*, *Diaptomus minutus* et autres sont grands et clairs, alors que ceux qui sont caractérisés par *Tropocyclops prasinus mexicanus*, *Diaptomus oregonensis* et autres sont plus petits et ont des eaux moins claires. Nous mettons ces schémas en contraste avec ceux extraits de mêmes données à l'aide de techniques plus subjectives. Dans la région de Killarney, Ontario, ayant à subir la contrainte des acides, nous prédisons que les lacs dominés par *D. minutus* seront acides, petits et clairs, alors que ceux dominés par *Diaphanosoma leuchtenbergianum*, *Bosmina longirostris*, *Mesocyclops edax* et autres seront moins clairs, plus grands et à pH plus élevé. Dans les lacs d'Haliburton, Ontario, nous prédisons que ceux dominés par *Diaptomus oregonensis*, *M. edax* et *Ceriodaphnia lacustris* seront petits et productifs, alors que ceux dominés par *Diaptomus minutus*, *D. sicilis*, *B. longirostris* et *Daphnia dubia* seront plus grands et moins productifs. Nous discutons de l'utilité de la technique et de certaines modifications.

Received August 26, 1976
Accepted March 15, 1977

Reçu le 26 août 1976
Accepté le 15 mars 1977

Printed in Canada (J4531)
Imprimé au Canada (J4531)

EMPIRICALLY determined relationships between the abundance of an indicator species and various physical and chemical aspects of its environment have provided a basis for drawing inferences about the history, quality, successional status, etc. of a variety of ecological habitats. An alternative to basing such inferences on knowledge of a few key indicator species is to use information on associations of species, or communities, for it can be argued that patterns of variability in a large group of species provide more information about the habitat than does variation in a single species. In freshwater ecology such an approach has been used to relate the developmental history of lakes to variations in their chydorid cladoceran communities (Goulden 1969), to relate changes in diatom communities to the deterioration of their habitat (Patrick et al. 1954, 1968), and to demonstrate pollution-related structural changes in protozoan communities (Cairns et al. 1972). However, in these and similar studies detailed community data comprising numerical abundances of many species have been summarized by a single index of community structure, variations in which have formed the basis for the analysis. An analysis of the raw data matrix, which may include abundances of several species for each of several habitats or points in time, necessitates the use of multivariate statistical techniques (Lambert and Dale 1964; Goodall 1970; Williams 1971; Kershaw 1973; Orloci 1975).

Principal component and cluster analyses have been successfully applied to marine zooplankton community data with a view to identifying species associations and characterizing them in terms of hydrographic and geographic variables (Williamson 1961; Fager and McGowan 1963; Cassie 1963; Colebrook 1964; Angel and Fasham 1973, 1974, 1975). The purpose of this study is to extend these analyses so that data on the structure of limnetic crustacean zooplankton communities can be used to make predictions about the limnological characteristics of some inland Ontario lakes. The analysis (a) groups lakes that have similar zooplankton communities, (b) identifies the species of these communities, (c) determines the limnological attributes common to the lakes of each group, and (d) combines these steps into a simple model predicting the limnological characteristics of a lake from a sample of its zooplankton community.

Materials and Methods

RAW DATA

Three comparable data matrices will be analyzed; one from the relatively undisturbed ELA lakes in northwestern Ontario composed of 49 lakes and 32 attributes (6 limnological variables and 26 zooplankton species); one from the acid-stressed Killarney lakes, Ontario, composed of 60 lakes and 45 attributes (22 limnological variables and 23 species); and one from the Haliburton lakes, Ontario, which show variation in phosphorus loading and concentration, composed of 19 lakes and 38 attributes (13 limnological variables and 25 species). For each lake in a survey a midsummer limnetic crustacean zooplankton sample and a series of standard physical and chemical measurements were taken.

Patalas (1971) presented data on 45 lakes in the Experimental Lakes Area (ELA) of northwestern Ontario including six physical and chemical variables and the percentage abundance of 28 crustacean zooplankton species. Zooplankton samples, collected during September 1967 and in July and August 1968, consisted of vertical hauls taken during daylight from near lake bottom to surface with a modified Clarke-Bumpus sampler (1968) or a large Wisconsin net (1967). All lakes were sampled once except four that were sampled twice (once each in 1967 and 1968) to give a total of 49 samples. The lakes are in acid-granite basins on the southwestern part of the Precambrian Shield. For the purposes of this study zooplankton abundances were converted from percentages to proportions and two species that occurred only in single lakes were eliminated. Further descriptions of the lakes and a map of the ELA area are in volume 28(2) of this journal.

Limnological data from 47 lakes lying in a series of quartzite ridges in Killarney Provincial Park on the northeast shore of Georgian Bay, Ontario, include 14 physical and 8 chemical variables; some of these data appear in Sprules (1975a), some in Harvey (1975), and the remainder are available on request from the author. Proportionate numerical composition of the zooplankton communities in these lakes (Sprules 1975a) is based on bottom-to-surface vertical hauls taken during daylight at the point of maximum lake depth with a large conical townet from July to September 1972 and 1973. Some lakes were visited only once, some were sampled more than once per summer, and some were sampled on the same day at different locations to give a total of 60 samples. Five species that occurred in single lakes were eliminated prior to the analysis. Sprules (1975a) and Harvey (1975) present a map of the Killarney region and Beamish and Harvey (1972) present a detailed description of the area.

Limnological data for the Haliburton lakes (Dillon and Rigler 1974; Dillon 1974), which are all part of or close to the Gull River drainage system in southern Ontario, were collected between May 1971 and December 1972. Thirteen lakes are included, 3 of which are subdivided into major basins, to give a total of 19 water bodies. Most of these lie in Precambrian granite or Precambrian sediments but four (Talbot, Raven, Cameron, and Fourmile) lie in Ordovician dolomitic limetsone. Zooplankton data for these lakes (available from the author) were collected August 27–29, 1973 during daylight at point of maximum

depth in each lake or major basin. Each lake was visited once only when a vertical haul from near bottom to surface was taken with a conical townet of 25 cm mouth diameter and 80-μm nylon mesh. Zooplankton counting techniques are as outlined by Sprules (1975a). A map and description of this study area are presented by Dillon and Rigler (1974).

Statistical Analyses

The basic multivariate statistical technique used here is principal component analysis (PCA). Although Morrison (1967) and Cooley and Lohnes (1971) give good presentations of the statistical features of PCA and Cassie (1972), Colebrook (1964), and Orloci (1975) show practical applications, a brief summary of the procedure as applied here will be given.

The data from each survey, recorded in a lake-by-species matrix of proportionate abundances, were normalized before analysis by application of the arc sine square root transformation (Sokal and Rohlf 1969). The matrix of covariances between species was calculated, thus standardizing the normalized abundances by subtraction of species means. This preserves the variability of individual species (Angel and Fasham 1973; Pielou 1969; Williamson 1972), which is considered here to be an important indicator of environmental differences. Principal component analysis summarizes the information in the covariance matrix in terms of new components, a small number of which account for most of the variation. From this simplification one can formulate hypotheses about the causes of variation in the system.

The basic effect of the analysis is to change the original lake-by-species matrix into a lake-by-component matrix where the number of components is much smaller than the number of species. Each component, a simple linear compound of the transformed proportionate abundances, has an associated eigenvalue giving the amount of variation in species accounted for by component, and an eigenvector of component coefficients giving the weighting of each species in the linear compound. Successive components account for unique, progressively smaller portions of the total variation in species, the first two or three together usually accounting for most of the variation. The variation summarized by a particular component is the variation in abundance of those species having high positive and negative correlations with that component. Note that it is variation in species abundance and not simply the magnitude of abundance that is important. Rare and common species alike can have high correlations with a component so long as their abundances vary greatly over the lakes.

The interrelations among lakes can be displayed in a bivariate plot of the value (= score) for each lake on components 1 and 2 (PC1, PC2). The score of a lake on a component is the sum of products of the transformed proportionate abundance for each species times its corresponding component coefficient (from the eigenvector). Lakes that have similar zooplankton associations will form a cluster on this graph. Superposition of a minimum distance tree (Gower and Ross 1969) computed from a taxonomic distance matrix between lakes (Sneath and Sokal 1973) will show up any distortions in interlake relations resulting from the reduction in dimensionality characteristic of principal component ordination. The unweighted pair-group clustering method using arithmetic averages (Sneath and Sokal 1973) with euclidean distance as a measure of interlake similarity was also used to help identify lake groupings. This clustering technique consistently yielded the best representation of relations among lakes as measured by the cophenetic correlation (Sneath and Sokal 1973). Although the clustering and distance tree analyses used are quite distinct from principal component analysis, concordance among the three techniques strengthens the interpretation made of the data (Schnell 1970).

Since the components can be characterized in terms of species, the composition of the zooplankton community common to a cluster of lakes is determined by the position of the cluster on the ordination graph. A limnological interpretation of this pattern can be obtained by examining Spearman's rank correlations (Sokal and Rohlf 1969) between the limnological variables and the component scores. Variation along a component is related to those limnological characteristics having high positive and negative correlations with that component.

Using the results of this analysis as a simple model, an independently selected lake can, on the basis of a sample of its zooplankton community, be related to the principal components by its scores on them and then be characterized limnologically by the environmental interpretation given to the component.

All of these statistical analyses were done at the University of Toronto computing center using a statistical package for numerical taxonomy called NTSYS.

Results and Discussion

Experimental Lakes Area (ELA)

The first three principal components from Patalas' (1971) data of the proportionate numerical abundance of 26 species in 49 lakes account for a total of 60.7% of the variance in the data, the first component accounting for 35.6% of the variance, the second for an additional 13.2%, and the third for the remaining 11.9%. *Diaptomus minutus*, *Cyclops bicuspidatus thomasi*, *Epischura lacustris*, *Daphnia galeata mendotae*, and *Limnocalanus macrurus* have significant positive correlations with the first component (Table 1), while *Tropocyclops prasinus mexicanus*, *Diaptomus oregonensis*, *D. leptopus*, and *Diaphanosoma brachyurum* have significant negative correlations with this component. Thus, lakes with relatively high abundances of the first five species and relatively low abundances of the last four

TABLE 1. Eigenvectors and correlations of species abundances with components 1 and 2 for ELA lakes.

	Principal component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Diaptomus minutus Lilljeborg	.530	.80[a]	.390	.36[b]
Cyclops bicuspidatus thomasi Forbes	.537	.79[a]	.067	.06
Epischura lacustris Forbes	.071	.41[c]	.093	.33[b]
Daphnia galeata Sars *mendotae* Birge	.071	.37[c]	−.044	−.14
Limnocalanus macrurus Sars	.005	.30[b]	−.002	−.07
Daphnia longiremis Sars	.012	.26	.005	.07
Diaptomus sicilis Forbes	.069	.25	−.015	−.03
Daphnia galeata mendotae (× *thorata* Forbes)	.039	.24	.010	.04
Senecella calanoides Juday	.005	.22	—[d]	−.02
Leptodora kindtii (Focke)	.004	.22	−.001	−.03
Diaphanosoma leuchtenbergianum Fischer	.053	.21	.032	.08
Chydorus sphaericus (O. F. Müller)	.017	.16	−.029	−.17
Daphnia retrocurva Forbes	.027	.11	−.043	−.11
Daphnia catawba Coker	.007	.05	−.046	−.22
Cyclops vernalis Fischer	−.017	−.06	−.139	−.32[b]
Daphnia schødleri Sars	−.010	−.11	−.023	−.15
Orthocyclops modestus (Herrick)	−.052	−.13	−.112	−.17
Holopedium gibberum Zaddach	−.045	−.14	−.206	−.39[c]
Mesocyclops edax (Forbes)	−.078	−.18	−.396	−.56[a]
Daphnia pulex Leydig	−.006	−.18	.002	.04
Ceriodaphnia lacustris Birge	−.015	−.19	−.046	−.36[b]
Bosmina longirostris (O. F. Müller)	−.071	−.25	−.215	−.47[a]
Diaphanosoma brachyurum (Liéven)	−.079	−.29[b]	−.018	−.04
Diaptomus leptopus Forbes	−.168	−.38[c]	−.024	−.03
Diaptomus oregonensis Lilljeborg	−.174	−.41[c]	−.346	−.49[a]
Tropocyclops prasinus mexicanus Kiefer	−.574	−.79[a]	.653	.55[a]

[a]Probability (P) of obtaining observed product–moment correlation if true value is zero (two-tailed test) < .001; [b]P < .05; [c]P < .01; [d]less than .001.

will have high scores on PC1; conversely, lakes with relatively low abundances of the first five species and relatively high abundances of the last four will have low scores on this component. As PC1 accounts for the single largest proportion of variance in the data, it can be concluded that the major difference among the ELA lakes is related to variations in abundance of these nine species. *Diaptomus minutus*, *C.b. thomasi*, and *T.p. mexicanus* are the most important species in this regard, for they have the highest correlations, regardless of sign, with PC1. The fact that *T.p. mexicanus*, *D. oregonensis*, *D. leptopus*, and *Diaphanosoma brachyurum* all have similar significant correlations with PC1 indicates that they have similar patterns of abundance over the lakes, i.e. they are associated in their distribution. The same is true for the other group of species.

A secondary independent source of variation in the data is summarized in the second principal component (Table 1), which separates lakes containing an association of three principal species, *T.p. mexicanus*, *Diaptomus minutus*, and *E. lacustris* from those containing *Mesocyclops edax*, *D. oregonensis*, *Bosmina longirostris*, *Holopedium gibberum*, *Ceriodaphnia lacustris*, and *Cyclops vernalis*. Because they have the highest correlations with PC2, *M. edax*, *T.p. mexicanus*, *D. oregonensis*, and *B. longirostris* are the most important discriminator species along this component.

The relations among the ELA lakes can be established by comparing the lake scores on the first two components (Fig. 1) with a cluster analysis of the zooplankton data (Fig. 2). The minimum distance tree in Fig. 1 indicates, for instance, that, despite its proximity to lake 164, lake 8 actually has a zooplankton community more similar to that of lake 99 than to that of lake 164. Cluster analysis (Fig. 2) gave a cophenetic correlation of 0.82 which suggests that the dendrogram is a good, but not perfect, representation of the true interlake relations. A comparison of Fig. 1 and 2 indicates the most realistic interpretation is that the lakes fall into four groups, the first two comprising four lakes (8,

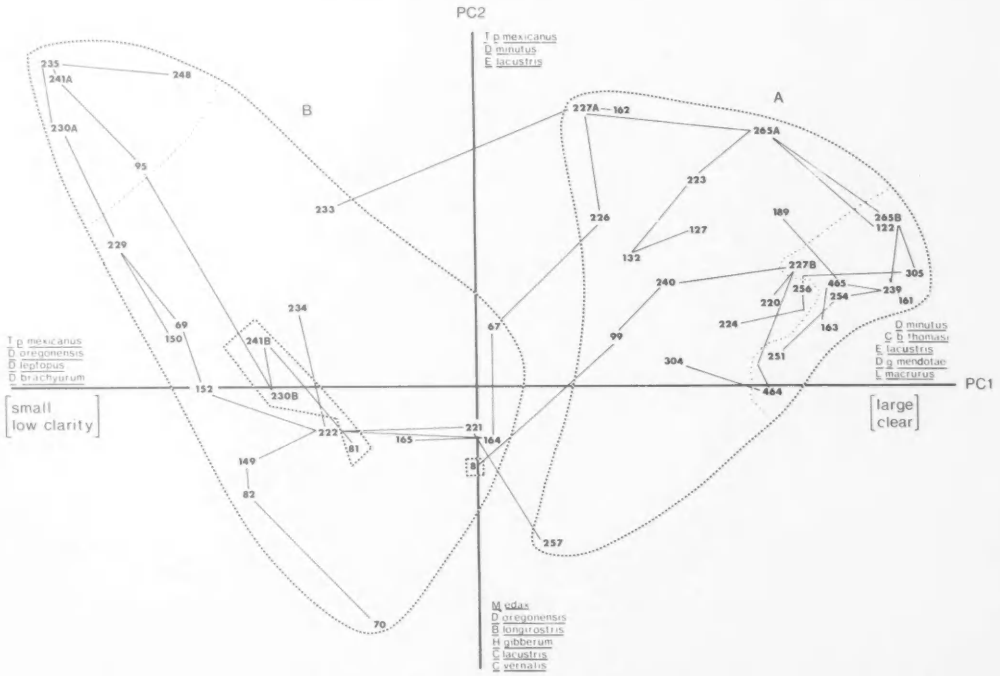

FIG. 1. Principal component ordination of ELA lakes. Lines joining lakes represent minimum distance tree. Dashed lines enclose lake groups determined from cluster and principal component analysis. Groups A and B are labeled. Dotted lines separate subgroups of lakes. Species and limnological labels on axes are from Tables 1 and 2, respectively.

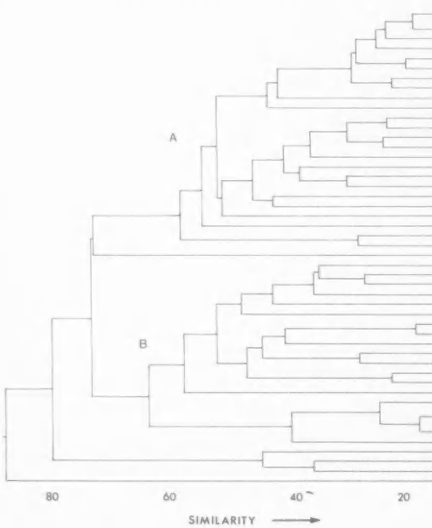

FIG. 2. Cluster analysis of ELA lakes. Similarity is measured by euclidean distance.

81, 241B, 230B) quite different from the others. The remaining 45 lakes fall into two large groups, A and B, with some suggestion that each of these is further split in two (Fig. 1).

Recalling the species characterizations of the components (Table 1), lakes in cluster A clearly differ, by virtue of high abundances of *D. minutus, C.b. thomasi, E. lacustris, Daphnia g. mendotae*, and *L. macrurus*, from lakes in cluster B, which have relatively high abundances of *T.p. mexicanus, Diaptomus oregonensis, D. leptopus*, and *Diaphanosoma brachyurum* (see species labels on axes in Fig. 1). The subdivision within groups A and B is based principally upon a contrast in the abundance of *T.p. mexicanus* with the abundances of *M. edax, Diaptomus oregonensis*, and *B. longirostris*. Analysis of Patalas' (1971) data reveals patterns consistent with this interpretation. Also, the uniqueness of lake 8 is clearly due to the unusually high (.86) proportionate abundance of *Orthocyclops modestus*. With this exception, *O. modestus* shows no consistent pattern of abundance over the lakes and hence its low correlations with the components (Table 1).

TABLE 2. Rank correlations between limnological variables and first and second principal components for ELA data.

	Component	
	1	2
Secchi disc visibility (m)	.68[a]	.01
Surface area (ha)	.64[a]	−.16
Maximum depth (m)	.60[a]	.22
Total dissolved solids ($mg \cdot \ell^{-1}$)	.21	−.07
Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)	−.36[b]	−.11
Color (Hazen units)	−.75[a]	−.28

[a]Probability (P) of obtaining observed rank correlation if true correlation is zero (two-tailed test) < .001; [b]$P < .05$.

Lakes 81, 241B, and 230B form a group on the basis of their comparatively high abundances of *D. leptopus*.

Finally, the limnological characteristics underlying these patterns emerge from an analysis of the rank correlations between component scores and the physical and chemical variables from the raw data (Table 2). Lakes that have large Secchi disc transparencies, surface areas, and maximum depths but low color and chlorophyl *a* values will have high scores on PC1 (group A); these are generally large, deep, clear lakes (limnological labels on axes of Fig. 1). By contrast lakes that are small, shallow, and of lower water clarity will have low scores on PC1 (group B). The absolute value of the correlations indicate the relative importances of the variables. Although PC2 accounts for some of the variance in species, no limnological variable is significantly correlated with it. This indicates that no measured lake characteristic is associated with variation in zooplankton communities along this component. The delineation of clusters of lakes is primarily for comparison with Patalas' (1971) analysis (see below) and a more realistic approach is to think of these patterns in community composition and limnological characteristics as continua along the principal components.

In terms of the original intent of this study then, the components can serve as discriminators of lake type. One has simply to obtain a midsummer limnetic crustacean zooplankton sample from an independently selected lake from the ELA lake survey, enumerate the species, and calculate the lake score on PC1 (using the species abundances and the eigenvector as outlined in Materials and Methods). This determines the location of the lake along the size–water-clarity continuum which characterizes the first component. Similar calculations will locate the lake on the second component which is presumably interpretable in terms of some unmeasured limnological continuum. According to one's own specific requirements, a critical value (or values) of component score can be set that separates lakes into appropriate categories. For the ELA data, for instance, a score on PC1 of about 5.0 (just right of the intersection with PC2 in Fig. 1) could serve as a division between deep, clear lakes and shallow, turbid lakes. Of course the reliability of such a discriminator will be related to the eigenvalues of the components and the magnitude of the correlations between components and species abundances and between components and limnological variables. This is intended as a first approach to lake characterization from zooplankton communities and some suggestions for improvements will be given below.

Some important similarities and differences exist between the ELA lake classification presented here and that originally proposed by Patalas (1971). Although we both began with the same raw data, Patalas formed his lake groups primarily by examining the distributions of dominant species (>10% of total crustacean numbers) "and the presence of some or other indicator species" (Patalas 1971, p. 237), whereas I have used objective multivariate statistical criteria. We have both identified four groups of lakes although Patalas classified a number of the lakes as intermediate types. In general, he has separated those lakes dominated by *T.p. mexicanus* from those dominated by *D. minutus* and *C.b. thomasi*, which, with the additional involvement of six other species, is the same contrast occurring along the first component in this study. Thus, my group A includes Patalas' Types I and II, while my group B includes all of his Type III lakes. By contrast, some of his Type II/III lakes fall in my group A, whereas others fall in my group B. Patalas further subdivides the *C.b. thomasi–D. minutus* lakes into Type I lakes, which also include *L. macrurus* and *Senecella calanoides*, and Type II lakes, which do not. On the other hand, PCA further subdivides the *D. minutus–C.b. thomasi* lakes along PC2 by contrasting the distribution of *T.p. mexicanus* and some other species with that of *M. edax*, *D. oregonensis*, *B. longirostris*, and some other species (Fig. 1). In addition, Patalas subdivides his *T.p. mexicanus* lakes into Types III and IV by contrasting the distribution of *D. oregonensis* with those of *D. leptopus* and *O. modestus*. However the fact that *D. oregonensis* and *D. leptopus* have similar negative correlations with PC1 (Table 1) suggests that statistically their distributions over the lakes are similar and thus cannot serve to separate lake types. Patalas

TABLE 3. Eigenvectors and correlations of zooplankton abundances with components 1 and 2 for Killarney lakes.

	Principal component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Diaphanosoma leuchtenbergianum	.215	.66[a]	−.142	−.24
Bosmina longirostris	.346	.64[a]	.605	.84[a]
Mesocyclops edax	.193	.60[a]	−.249	−.27[b]
Cyclops bicuspidatus thomasi	.275	.54[a]	−.593	−.63[a]
Daphnia retrocurva	.067	.45[a]	−.094	−.35[c]
Tropocyclops prasinus mexicanus	.077	.37[c]	−.079	−.20
Diaptomus oregonensis	.086	.37[c]	−.190	−.45[a]
Leptodora kindtii	.007	.34[c]	−.013	−.34[c]
Daphnia galeata mendotae	.064	.34[c]	−.151	−.44[a]
Diaptomus reighardi Marsh	.057	.33[c]	.017	.05
Ceriodaphnia reticulata (Jurine)	.021	.30[b]	.008	.06
Holopedium gibberum	.119	.28[b]	.330	.42[a]
Daphnia longiremis	.039	.27[b]	−.077	−.29[b]
Daphnia ambigua Scourfield	.021	.26[b]	−.022	−.15
Senecella calanoides	.005	.25	−.008	−.22
Cyclops scutifer Sars	.012	.17	−.021	−.16
Epischura lacustris	.030	.13	−.062	−.14
Polyphemus pediculus (L)	.003	.08	.033	.50[a]
Daphnia sp.	.001	.04	−.008	−.17
Daphnia catawba	−.002	−.01	−.007	−.02
Daphnia pulicaria Forbes	−.007	−.01	.055	.19
Orthocyclops modestus	−.017	−.10	−.02	−.07
Diaptomus minutus	−.823	−.99[a]	−.044	−.03

[a]*Probability (P) of obtaining observed product–moment correlation if true correlation is zero (two-tailed test)* < .001; [b]$P < .05$; [c]$P < .01$.

Type IV lakes appear to be quite variable in community composition, for they include the rather distinctive lakes 8, 241B, 230B, and 81 (my first two small groups) as well as a number of my group B lakes. Finally a number of species (e.g. *E. lacustris, Daphnia g. mendotae, M. edax, B. longirostris*) of importance in the component analysis as discriminators of lake type are of no importance in Patalas' classification.

The net effect of the differences between the two approaches is the emergence of two dissimilar lake classifications, which if used, for instance, as a basis for assigning lakes to experimental groups, would probably lead to very different results. Of particular interest are the 1967 and 1968 samples from each of lakes 227, 230, 241, and 265. Patalas separates the 1967/1968 pair of samples from lake 227 into Types II/III and II, respectively, but in each of the remaining cases considers the members of the pair as the same Type. On the other hand I have clearly separated lakes 230A and 241A (1967 samples) from lakes 230B and 241B (1968 samples) (Fig. 2). There is also some suggestion (Fig. 1) that lakes 227A and 265A are quite different from their 1968 counterparts, 227B and 265B. Thus, in contrast to the subjective approach, the statistical analysis identifies annual variations in zooplankton community structure which may be important; this will be discussed below.

There is also a major difference in the limnological characterizations of the lake groups, for although both Patalas and I have recognized the importance of lake size and depth, Patalas does not use water clarity, which, as measured by color and Secchi disc transparency, has the largest correlation with PC1 and is therefore the most important limnological discriminator between lake groups.

KILLARNEY LAKES

The Killarney lakes have been subjected to acid rains in the past (Beamish and Harvey 1972) which have created considerable variations in the surface pH from one lake to another. There have been associated effects on the limnetic crustacean zooplankton communities (Sprules 1975a, b). Principal component analysis of data from these lakes will provide a comparison with

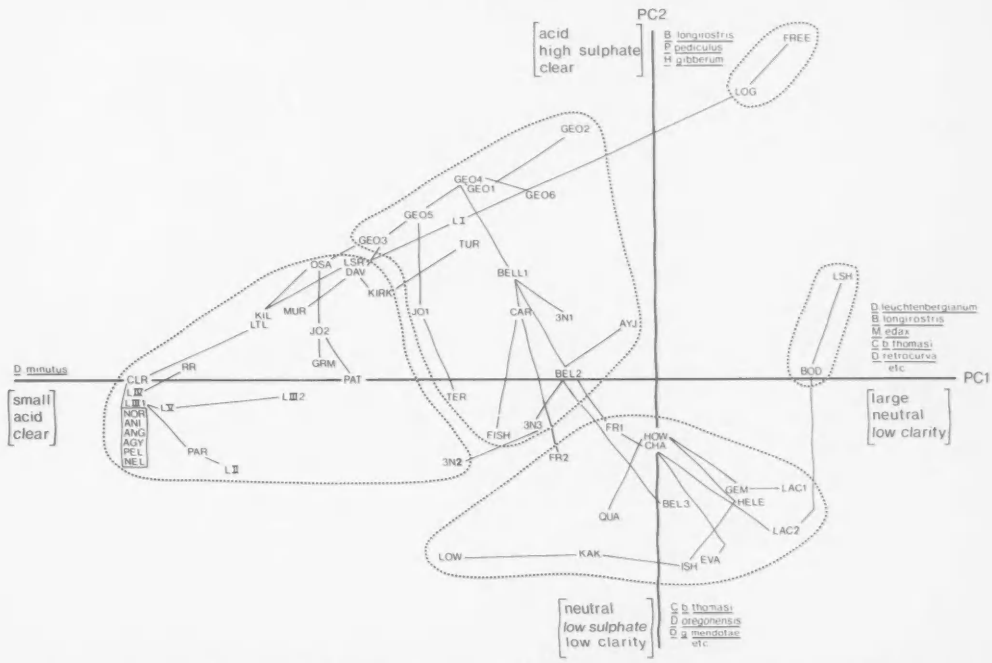

FIG. 3. Principal component ordination of Killarney lakes. Lines joining lakes represent the minimum distance tree. Dashed lines enclose groups of lakes identified in the cluster analysis. The six lakes in the box all have the same coordinates. Species and limnological labels on the axes are from Tables 3 and 4, respectively. Lake abbreviations: ANG, Anguish; AGY, Agony; ANI, Animus; AYJ, A.Y. Jackson; BEL1, *Bell, 19.7.72, SW basin*; BEL2, Bell, 21.7.72, midbasin; BEL3, Bell, 21.7.72, N basin; BOD, Bodina; CAR, Carlyle; CHA, Charlton; CLR, Clearsilver; DAV, David; EVA, Evangeline; FISH, Fish; FR1, Frood, *11.9.72*; *FR2, Frood, 10.9.72*; *FREE, Freeland*; *GEM, Gem*; *GEO1, George, 15.7.72, S basin*; GEO2, George, 15.7.72, N basin; GEO3, 20.7.72, N basin; GEO4, George, 30.7.72, N basin; GEO5, George *16.8.72; N Basin*; *GEO6, George, 16.9.72, N basin*; *GRM, Great Mountain*; *HOW, Howry*; *HELE, Hele*; ISH, Ishmael; JO1, Johnnie, 7.7.72, N basin; JO2, Johnnie, 4.7.72, central basin; KAK, Kakakise; KIL, *Killarney*; *KIRK, Kirk*; *LI, LII etc., Lumsden 1, 2 etc. (LIII1, 4.7.72, LIII2, 15.8.73)*; *LAC1, LaCloche*, 29.8.72; LAC2, LaCloche, 3.9.72; LOG, Logboom; LOW, Low; LSH, Little Sheguindah; LSR, Lesser Mountain; LTL, Little Mountain; MUR, *Muriel*; NEL, *Nellie*; *NOR, Norway*; *OSA, O.S.A.*; *PAR, Partridge*; PAT, Patten; PEL, Pellucid; QUA, Quartzite; RR, Ruth-Roy; TER, Terry; 3N1, Threenarrows, 17.8.73, N basin; 3N2, Threenarrows, 17.8.73, W basin; 3N3, Threenarrows, 17.8.73, E basin; TUR, Turbid.

the analysis of the relatively undisturbed ELA lakes.

The first three principal components from an analysis of the distribution of 23 zooplankton species in 60 Killarney lakes accounted for 74.3% of the variance in the data, the first accounting for 50.1%, the second for 14.9%, and the third for 9.3%. The first component summarizes variation from communities with relatively high abundances of *Diaphanosoma leuchtenbergianum*, *B. longirostris*, *M. edax*, and 11 other species to those with relatively high abundances of *Diaptomus minutus*. The second component represents variation from relatively high abundances of *B. longirostris*, *Polyphemus pediculus*, and *Holopedium gibberum* to relatively high abundances of *C.b. thomasi* and six other species (Table 3). Although cluster analysis separates out some lake groups, the ordination of the lakes and the minimum distance tree (Fig. 3) indicate that it is more realistic to consider that PC1 represents a continuum in plankton community variation. Variation in the abundance of *D. minutus*, which is almost perfectly negatively correlated with PC1 (Table 3), is the most important pattern in the zooplankton data.

Correlations with limnological variables indicate that variation along PC1 is from circumneutral lakes of relatively low water clarity to small, clear, acid lakes (Table 4, Fig. 3). A cer-

TABLE 4. Rank correlations between limnological variables and the first and second principal components for Killarney lakes.

	Component	
	1	2
pH	.63[a]	−.54[a]
Length (km)	.35[b]	−.06
Mean effective length (km)	.33[b]	−.06
Island perimeter (km)	.32[c]	−.04
Total hardness (mg·ℓ^{-1})	.31[c]	−.10
Lake perimeter (km)	.31[c]	−.03
Surface area (ha)	.31[c]	−.03
Max effective breadth (km)	.30[c]	−.01
Vol development	.28[c]	−.08
Mean breadth (km)	.26[c]	−.07
Breadth (km)	.26[c]	−.07
Shoreline development	.19	0.0
Vol (m^3)	.17	−.02
Silicon (mg·ℓ^{-1})	.09	.13
Total dissolved solids (mg·ℓ^{-1})	.01	−.16
Sulphate (mg·ℓ^{-1})	0.0	.36[b]
Bicarbonate alkalinity (mg·ℓ^{-1})	−.03	−.08
Mean depth (m)	−.03	−.12
Conductivity ($\mu\Omega$)	−.04	−.19
Maximum depth (m)	−.14	−.14
Total phosphate (mg·ℓ^{-1})	−.22	.17
Secchi disc transparency (m)	−.61[a]	.27[c]

[a]Probability (P) of obtaining observed rank correlation coefficient if true value is zero (two-tailed test) < .001; [b]$P < .01$; [c]$P < .05$.

tain amount of redundancy in the data is indicated by the large number of intercorrelated variables associated with PC1. Variations in acidity are also important along the second component, as are variations in sulphate concentration and, to a much lesser extent, variations in water clarity. It should be emphasized here that components of species abundance have been extracted from the data and they are orthogonal or uncorrelated. That pH and Secchi disc transparency are correlated with both components simply indicates that primary and secondary patterns in species abundances are both associated with variations in acidity and water clarity.

These results suggest that the acid stress experienced by the Killarney lakes is the major cause of variations in the structure of their zooplankton communities. The PCA thus provides a means of determining the acid stress to which a lake has been subjected from knowledge of its zooplankton community. The transformed relative abundances of individual species from a midsummer zooplankton sample in combination with the eigenvectors corresponding to the first and second principal components (Table 4) produces scores which locate a lake on the ordination. Its relative position is indicative of the degree to which the lake has increased in acidity. Combining this approach with my more detailed analysis of the zooplankton communities of these lakes (Sprules 1975a, b) I can say that lakes in the bottom cluster (Fig. 3) show no sign of acid stress, those in the central cluster show signs of moderate acid stress, and those in the left cluster show signs of serious acid stress. Again the reliability of the characterization is a direct function of the proportion of variation in species summarized by the components and of the degree to which species abundances and limnological variables are correlated with the components.

To get some idea of the stability of the position of a lake on the ordination in relation to sampling date and sampling site, multiple samples were taken from seven Killarney lakes. Two samples from LaCloche Lake taken at the same site 5 days apart are located close together, as are two from Frood Lake taken from one site on consecutive days (Fig. 3). Similarly, five samples from George Lake taken from one site at different times of the summer are in close proximity; the slightly varying positions represent the seasonal sequence of zooplankton communities from July 15 (George 2) through September 16 (George 6), 1972. The slightly different positions of two Lumsden III Lake samples taken in consecutive summers reflect annual variations in community structure. George 1 and George 2 samples, both taken July 15, 1972, are from different basins, yet are close neighbours on the ordination. On the other hand samples taken on the same day from different basins in Threenarrows and Bell lakes, and samples taken on different days from different basins in Johnnie Lake show less consistency of position (Fig. 3). This is perhaps not too surprising as limnological differences, and hence biological differences, between lake basins may be considerable. There thus appears to be some stability in zooplankton samples selected at different times of the summer (or different summers) from the same site, but differences between basins in a lake may be as important as differences between lakes.

HALIBURTON LAKES

The first three principal components from an analysis of the Haliburton zooplankton data accounted for 67.8% of the variance in the data, the first accounting for 32.6%, the second for 20.2% and the third for 15.0%. Variation along the first component is from communities in which *D. minutus*, *B. longirostris*, *Daphnia dubia*, and *Diaptomus sicilis* are relatively abundant to those

TABLE 5. Eigenvectors and correlations of zooplankton species abundances with components 1 and 2 for Haliburton lakes.

	Principal component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Diaptomus minutus	.658	.94[a]	.128	.14
Bosmina longirostris	.274	.70[a]	−.028	−.06
Daphnia dubia Herrick	.161	.55[b]	−.014	−.03
Diaptomus sicilis	.145	.55[b]	.177	.53[b]
Cyclops scutifer	.210	.45	.316	.54[b]
Epischura lacustris	.033	.44	.042	.44
Cyclops bicuspidatus thomasi	.201	.32	−.709	−.88[a]
Sida crystallina (O. F. Müller)	.020	.31	.023	.28
Polyphemus pediculus	.007	.27	−.011	−.33
Daphnia longiremis	.048	.16	−.188	−.48[b]
Chydorus sphaericus	.040	.11	.162	.36
Eucyclops speratus (Lilljeborg)	.001	.11	0.0	0.0
Senecella calanoides	.008	.04	−.059	−.24
Tropocyclops prasinus mexicanus	−.004	−.02	−.002	−.01
Daphnia retrocurva	−.029	−.12	−.073	−.23
Daphnia galeata mendotae	−.087	−.16	−.367	−.55[b]
Leptodora kindtii	−.007	−.23	.010	.26
Orthocyclops modestus	−.009	−.26	−.020	−.45
Holopedium gibberum	−.082	−.26	.094	.23
Cyclops vernalis	−.063	−.31	.071	.27
Diaphanosoma leuchtenbergianum	−.098	−.35	−.070	−.20
Ceriodaphnia lacustris	−.217	−.51[b]	.339	.63[c]
Diaptomus oregonensis	−.410	−.63[c]	−.08	−.01
Mesocyclops edax	−.331	−.79[a]	.031	.06

[a]Probability (P) of obtaining observed product–moment correlation coefficient if true value is zero (two-tailed test) < .001; [b]P < .05; [c]P < .01.

in which *M. edax*, *D. oregonensis*, and *Ceriodaphnia lacustris* are relatively abundant (Table 5, Fig. 4). Along the second component, variation is from communities with relatively high abundances of *C. lacustris*, *Cyclops scutifer*, and *D. sicilis* to those with relatively high abundances of *C. b. thomasi*, *Daphnia g. mendotae*, and *D. longiremis* (Table 5). Cluster analysis indicates two major groups of lakes and two smaller ones (Fig. 4), a pattern consistent with the principal component ordination. Talbot Lake is different from all other lakes for, in addition to the comparatively high abundances of *M. edax* and *Ceriodaphnia lacustris* that account for its position on the ordination, it is characterized by an unusually high proportionate abundance (.22) of *Holopedium*. Dillon and Rigler (1974) also identified Talbot Lake as unusual (extremely shallow with no stream inflow), for it was the only one of these lakes that did not fit their nutrient budget model.

With its high positive correlations with mean depth, Secchi disc transparency, and volume and a high negative correlation with total spring phosphorus concentration (Table 6), the first component can be generalized as a size–productivity component (variation is from shallow, productive lakes at the negative end of PC1 to deep, unproductive lakes at the positive end). All significant correlations with PC2 are negative ones involving variables that measure supply rate and flushing rate, suggesting that this component is inversely related to nutrient (in this case phosphorus) loading.

Even though they are separated simply by a deep channel, South Bay and Haliburton lakes are placed in separate groups by the PCA (Fig. 4). This is clearly because of the differences in their zooplankton communities, which are due to the associated differences in their phosphorus loading and flushing rates. It is encouraging that the resolving powers of the PCA are sufficient to identify lake differences which might otherwise have been overlooked.

These Haliburton lakes vary in productivity and nutrient-loading characteristics, which, although partially related to lake and catchment basin morphometry, are also functions of human

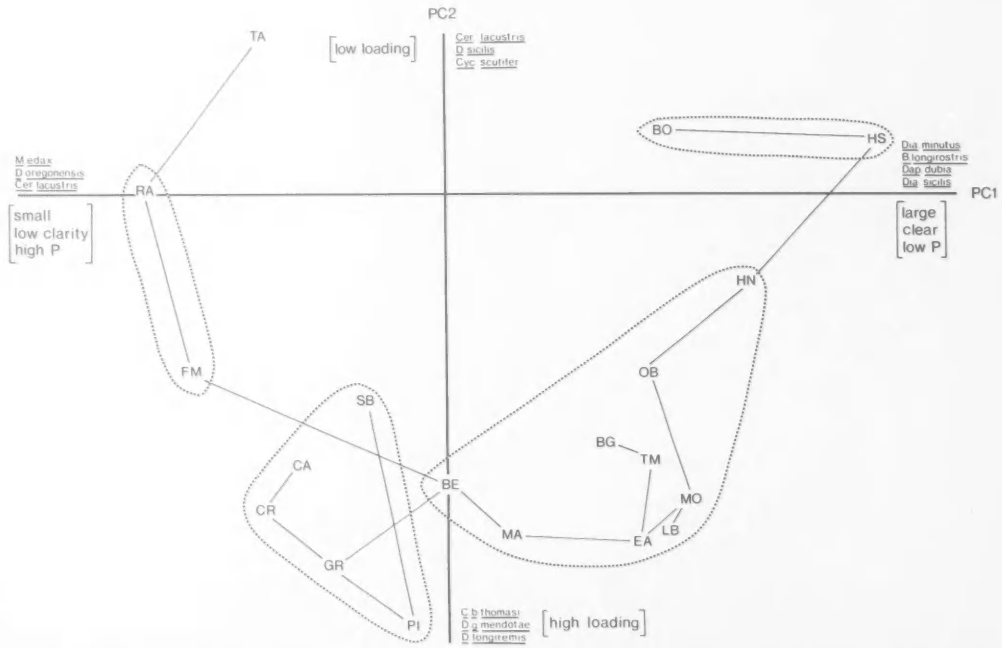

FIG. 4. Principal component ordination of Haliburton Lakes. Lines joining lakes represent minimum distance tree. Dashed Lines enclose lake groups determined from cluster and principal component analysis. Species and limnological labels on axes are from Tables 5 and 6, respectively. Lake abbreviations: BE, Beech; BO, Bob; BG, Boshkung; CA, Cameron; CR, Cranberry; EA, Eagle; FM, Four Mile; GR, Green; HN, Haliburton; HS, Halls; LB, Little Boshkung; MA, Maple; MO, Moose; OB, Oblong; PI, Pine; RA, Raven; SB, South Bay; TA, Talbot; TM, Twelve Mile.

TABLE 6. Rank correlations between limnological variables and first and second principal components for Haliburton lakes.

	Component	
	1	2
Mean depth (m)	.80[a]	.18
Avg summer Secchi disc transparency (m)	.76[a]	.02
Lake vol (m^3)	.56[b]	.17
Lake surface area (km^2)	.34	.14
Shoreline length (km)	.24	.31
Annual discharge (m^3)	.17	−.59[c]
Drainage area (km^2)	.15	−.61[c]
Drainage area/lake surface area	−.01	−.75[a]
Annual phosphorus supply (kg)	−.02	−.34
Avg summer chlorophyll *a* ($mg \cdot m^{-3}$)	−.18	−.12
Phosphorus loading ($mg \cdot m^{-2} \cdot yr^{-1}$)	−.27	−.50[b]
Flushing rate (yr^{-1})	−.34	−.65[c]
Total spring phosphorus ($mg \cdot m^{-3}$)	−.80[a]	−.15

[a]Probability (P) of obtaining observed rank correlation if true value is zero (two-tailed test) < .001; [b]$P < .05$ [c]$P < .01$.

activities (Dillon and Rigler 1975). The PCA makes it possible, on the basis of a midsummer zooplankton sample, to characterize an independently selected lake in terms of these production related variables. Lakes that fall into the lower right quadrant of Fig. 4 are deep, unproductive lakes with high rates of turnover and phosphorus loading. On the other hand, lakes falling into the upper left quadrant will be comparatively shallow and productive lakes with low nutrient supply and flushing rates.

General Discussion

The objective of this study was to develop a model for relating limnological characteristics of lakes to the structure of their limnetic crustacean zooplankton communities. The first part of the analysis, namely the ordination of lakes from the species variance–covariance matrix, is straightforward. Each lake can be unambiguously located by its score on each component, the species characterizing a component can be determined from their correlations with the component, and

a measure of the proportion of species variance summarized by the components is provided. It may be difficult to assign every lake to a cluster of similar lakes, but this is often an unnecessary and even unwarranted step in the context of this study. In other words, the identification of the major lines of variation in multispecies data is accomplished by the component analysis. Two variations on this approach should be considered: (a) instead of basing the analysis on the species covariance matrix, use the correlation matrix, which will effectively give equal weight in the analysis to variation in the abundances of common and rare species; and (b) instead of using numerical or proportionate species abundances, use presence–absence data. My own preliminary results suggest that for both of these modifications only a small proportion of the species variance is summarized in even the first four or five components, i.e. the data reduction capacity of the analysis is much poorer. In PCA one must also evaluate the advantages and disadvantages of data normalization and standardization. Many of these modifications will depend on the requirements of the individual. For the purposes discussed here the covariance matrix with data normalization is probably most efficient and informative.

The second step in the analysis, in which a relation between the components and the limnological variables is established, can probably be improved. Part of the problem could be inherent in the data, for there may not be readily interpretable limnological correlates of each component. Nothing can be done about this. A major problem with the simple rank correlations used here is the difficulty of establishing the relative importances of the variables where intercorrelations among them are high (e.g. all of the supply and flow rate variables negatively correlated with PC2 in the Haliburton data). In addition, it is difficult on the basis of simple correlations to determine the amount of variance in the limnological characteristics actually summarized by a component. Two other statistical techniques, multiple regression (Cooley and Lohnes 1971; Kendal 1968) and canonical correlation (Pielou 1969; Cassie 1972; Barkham and Norris 1970; Cooley and Lohnes 1971), may be useful at this stage of the analysis. The former eliminates redundant or highly correlated independent variables (limnological) to provide the smallest battery of these variables accounting for the greatest variance in the dependent variable (lake scores). This relation provides a quantitative limnological characterization of lakes as opposed to the qualitative one of correlation. However, regression is a parametric statistical technique which is most efficient when the independent variables are normally distributed and entirely uncorrelated with one another, situations rarely arising in ecological data. Canonical correlation provides information on the degree of relation between patterns in species distributions and limnological patterns but it requires that the lakes-by-limnological-variables matrix has more rows (lakes) than columns so that the inverse of the matrix is defined.

The approach presented here — principal component analysis of species and rank correlations between components and limnological variables — is intended as a first attempt at limnological characterization of lakes from knowledge of zooplankton communities. Insofar as it can provide information about a lake from comparatively easily and economically collected zooplankton data, it is a worthwhile technique. If the reliability of zooplankton communities in general as limnological indicators is not high, then the approach outlined here is probably all that is warranted. On the other hand, further analyses may indicate that zooplankton communities can characterize lakes with a high degree of confidence. If this is the case, then the modifications to the analytic technique which I have suggested should be investigated.

Although the three lake surveys used for this analysis come from separate parts of the Canadian Shield and show variation in different limnological aspects, to some extent the same species of zooplankton consistently serve to characterize the different lakes. *Bosmina longirostris*, *Daphnia g. mendotae*, *Diaptomus minutus*, *D. oregonensis*, *C.b. thomasi*, and *M. edax* have significant correlations with one or both components in all three surveys and *T.p. mexicanus*, *Ceriodaphnia lacustris*, *Holopedium*, and *Daphnia longiremis* are important in two of the three surveys. In the ELA and Haliburton lakes *Diaptomus minutus* is associated with large, deep, clear lakes, although in the Killarney lakes it is characteristic of small, acid, clear lakes. *Diaptomus oregonensis* is characteristic of comparatively shallow, productive lakes in the ELA and Haliburton areas. Thus, as I have suggested elsewhere (Sprules 1975a), some crustacean zooplankters may characterize particular kinds of lakes over much of the Canadian Shield. However, this is not true for many of the important species in this study and it must be borne in mind that each analysis is specific to a particular geographic region, i.e. the model for lake characterization developed for the ELA lakes cannot be used for the Haliburton lakes.

The question of the validity of using single

midsummer zooplankton samples for lake characterization arises in this study. Samples taken at about the same time from the same site in some Killarney lakes were reasonably consistent, thus suggesting that single samples are representative of the plankton community at that point in time. However, some annual differences in community structure (ELA lakes) and some interbasin differences (Killarney lakes) were important. Given the consistency of duplicate samples mentioned above, these differences may reflect variations in the limnological characteristics between basins and between years. With more detailed sampling data the principal component approach could clarify this. Seasonal differences in community structure may also be important (George Lake in the Killarney area). A slight modification of principal component ordination provides a means of displaying these temporal trends (Goff and Zedler 1972). In this, each lake could be sampled quarterly and the principal components calculated for the matrix of yearly mean or total abundances of each species for each lake. On a graph with the first two of these components as axes, every lake will be represented by four points, each one corresponding to a quarterly sample. If two lakes have distinct zooplankton communities, despite seasonal variations, the clusters of four points corresponding to each lake should be well separated. Overlapping of the clusters would suggest a closer relationship between the lakes than might have been deduced from once yearly samples. The use of this analysis is currently being assessed on another set of data.

There is the possibility that biological factors such as interspecific competition and/or size-selective predation account for some of the variability in community structure between lakes. However, in many instances in this study the correlations with limnological variables are quite high, suggesting either that biological interactions can at most account for a small amount of the left over variation or that they are correlates of the limnological variables. Given that prediction of lake type from knowledge of community structure is the major goal here, biological factors will thus be of minor importance. It is perhaps most likely that a certain group of species will tolerate particular limnological conditions, and biological factors account for variations in structure within these limits.

Acknowledgments

I thank Mr T. J. Carleton and Dr A. Baker for statistical advice, and Mr D. Gwynne and Mr G. Stirling for help with the Haliburton samples. Dr H. H. Harvey and Dr P. Dillon kindly provided unpublished data from the Killarney and Haliburton Lakes, respectively. Support from the Fisheries and Marine Service, Department of Fisheries and the Environment, is gratefully acknowledged. Funds were also provided by the National Research Council of Canada (Operating Grant No. A6388) and Erindale College, University of Toronto, for which I am grateful.

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Distribution and Abundance of Seals in the Eastern Beaufort Sea

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STIRLING, I., R. ARCHIBALD, AND D. DEMASTER. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. *J. Fish. Res. Board Can.* 34: 976–988.

The objectives of this study were: (1) to design a statistically reliable method for surveying ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) that could be repeated and, (2) to obtain baseline information on the distribution, abundance, and general biology of ringed and bearded seals in relation to other mammals in the pack-ice ecosystem of the eastern Beaufort Sea.

Because of the limitations encountered in aerial surveying during the period of optimum haul out, and the heterogeneous environment, we employed a stratified design incorporating a weighted linear regression model. Identical surveys, conducted from June 15 to 29, 1974 and from June 12 to 20, 1975, showed a significant decline in numbers of both seal species in 1975. This conclusion was supported by other independent observations. Observer bias in sighting and identifying the species of seals was tested for and rejected. Neither species was distributed randomly over the heterogeneous habitat but the degree of clumping was different. In general, bearded seals preferred shallower areas and ringed seals deeper ones.

When the seal population declined, the reproductive rates of both species dropped markedly and young of the year virtually disappeared from the population. The reduction in numbers of seals stimulated a major change in reproductive rates of the polar bears (*Ursus maritimus*) and arctic foxes (*Alopex lagopus*) that depend upon them for food, and the bear and fox populations decreased in size.

Some possible causes of the decline are discussed. This unprecedented variability in the stability of the marine ecosystem has serious management implications.

Key words: census techniques, *Phoca hispida*, *Erignathus barbatus*, seals, interspecific relationships, Beaufort Sea

STIRLING, I., R. ARCHIBALD, AND D. DEMASTER. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Board Can. 34: 976–988.

Cette étude avait comme objectifs: (1) mettre au point une méthode statistiquement fiable et répétable de recensement des phoques annulés (*Phoca hispida*) et des phoques barbus (*Erignathus barbatus*) et (2) obtenir des connaissances de base sur la distribution, l'abondance et la biologie générale des phoques annulés et barbus en relation avec les autres mammifères dans l'écosystème de la banquise dans la mer de Beaufort orientale.

A cause des limitations imposées au relevé aérien durant la période de remontée optimale sur la banquise, et à cause de l'environnement hétérogène, nous avons utilisé une méthode stratifiée incorporant un modèle de regression linéaire pondérée. Des recensements identiques, effectués du 15 du 29 juin 1974 et du 12 au 20 juin 1975 indiquent une diminution significative de l'abondance des deux espèces de phoques en 1975. D'autres observations indépendantes confirment cette conclusion. L'erreur systématique des observateurs dans le repérage et l'identification des espèces de phoques a été soumise à des tests et rejetée. Ni l'une ni l'autre des espèces ne sont réparties au hasard dans tout l'habitat hétérogène, mais le degré de rassemblement est différent. En général, les phoques barbus préfèrent les régions moins profondes, et les phoques annulés les régions plus profondes.

Avec le déclin de la population de phoques, le taux de reproduction des deux espèces diminue notablement, et les jeunes de l'année disparaissent virtuellement de la population. La

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Printed in Canada (J4498)
Imprimé au Canada (J4498)

diminution du nombre de phoques entraîne un changement majeur dans les taux de reproduction de l'ours polaire (*Ursus maritimus*) et du renard arctique (*Alopex lagopus*) qui en dépendent pour leur nourriture, et les populations d'ours et de renards diminuent de taille.

Les auteurs analysent quelques causes possibles du déclin. Cette variabilité sans précédent de la stabilité de l'écosystème marin a de sérieuses implications pour la gestion.

Received August 3, 1976
Accepted March 15, 1977

Reçu le 3 août 1976
Accepté le 15 mars 1977

WITH the prospect of large-scale oil exploration and subsequent production in the eastern Beaufort Sea, baseline data are required on the present status of all species that might be affected. Studies of the interrelationships of arctic mammals inhabiting the land-fast and pack ice suggest that the distribution, abundance, and productivity of polar bears (*Ursus maritimus*) and arctic foxes (*Alopex lagopus*) are controlled by the availability of seals (Stirling and Smith 1977).

The principle pinniped species in the eastern Beaufort Sea are the ringed seals (*Phoca hispida*) and the bearded seal (*Erignathus barbatus*). The walrus (*Odobenus rosmarus*) and harbour seal (*Phoca vitulina*) are regular visitors to the area (Harington 1966; Stirling 1974) but their numbers are too few to consider in this report.

The general biology of the ringed and bearded seals are described elsewhere (McLaren 1958a, b; Johnson et al. 1966; Burns 1967; Ivashin et al. 1972; Benjaminsen 1973; Smith 1973a; Stirling and Smith 1977).

There are few published data on seals in the Beaufort Sea. A limited amount of information on Inuit utilization is available in the Area Economic Surveys conducted by the Department of Indian Affairs and Northern Development (Abrahamson 1962; Usher 1965). Smith et al. (1973) and Smith and Geraci (1975) gave preliminary results of long-term physiological research on ringed seals in Amundsen Gulf. Smith and Stirling (1975) described ringed seal breeding habitat and discussed some of the aspects of seasonal variation in productivity. Stirling and Smith (1977) discussed the interrelationships of the mammals in the sea-ice habitat.

The objectives of this study were: (1) to design a statistically reliable method for surveying ringed and bearded seals, and (2) to obtain baseline information on the distribution, abundance, and general biology of ringed and bearded seals in the pack-ice ecosystem of the eastern Beaufort Sea.

Materials and Methods

Study Area

The study area was broadly defined as the Beaufort Sea, east of 140°W and south of 74°N, including the Amundsen Gulf (Fig. 1).

The area has an arctic maritime climate with coastal temperatures ranging from 25°C in June to < -40°C in January (Thompson 1962). Sea-ice formation begins in late September and the fast ice, predominantly 1st-yr ice, extends from 16 to 50 km offshore (Burns 1973). Ice cover is complete by November and continuous for a mean length of 280 days. Thermal factors and wind stresses cause periodic fracturing of the ice and the formation of leads (Burns 1973). Spring breakup of fast ice can be expected by mid-June to early July, opening a channel along the mainland coast and north along the west coast of Banks Island. In years of prolonged onshore winds, the drifting pack ice of the Beaufort Sea is driven landward, resulting in little navigable water. Alternatively, prevailing offshore winds keep the whole of the southern Beaufort Sea relatively ice free (Burns 1973).

The eastern Beaufort Sea is characterized by a shallow shelf extending outwards 80–110 km from the mainland coast (Henry 1975). The average depth across the shelf is < 50 m. North of the shelf the water depths vary from 450 m in the Amundsen Gulf area to > 3500 m north of Herschel Island (Burns 1973). West of Banks Island, Stefansson (1921) found that the coastal shelf extends some 160 km. Tides along the coastal Beaufort Sea have a maximum range of 0.8 m (Burns 1973) and are almost entirely masked by meteorological effects (Henry 1975).

At best, the Beaufort Sea supports a fairly low rate of primary and secondary biological production, seemingly limited by the available supply of nitrate and phosphate (Grainger 1975). Primary biological production is also directly influenced by the extent, duration, and snow cover of the sea ice, which in turn affects the amount of light reaching the photosynthetic organisms (Grainger 1975).

Aerial Survey Design

Ringed and bearded seals are most easily seen and counted when they are basking on the sea ice. The greatest number of seals haul out on the ice to molt in late June, immediately prior to breakup (McLaren 1958a; Smith 1973a, b). There is also a diurnal fluctuation in the number of seals hauled out on the ice with a maximum in early to midafternoon (Burns and Harbo 1972; Smith 1973a). However, even during this optimal period, there is no accurate way of correlating the number of seals hauled out with the total number present. Despite this failing and for lack of a better quantitative replacement, aerial surveying continues, with a variety of designs (Burns and Harbo 1972; Smith 1973b; this study). To maximize the number of seals counted while they

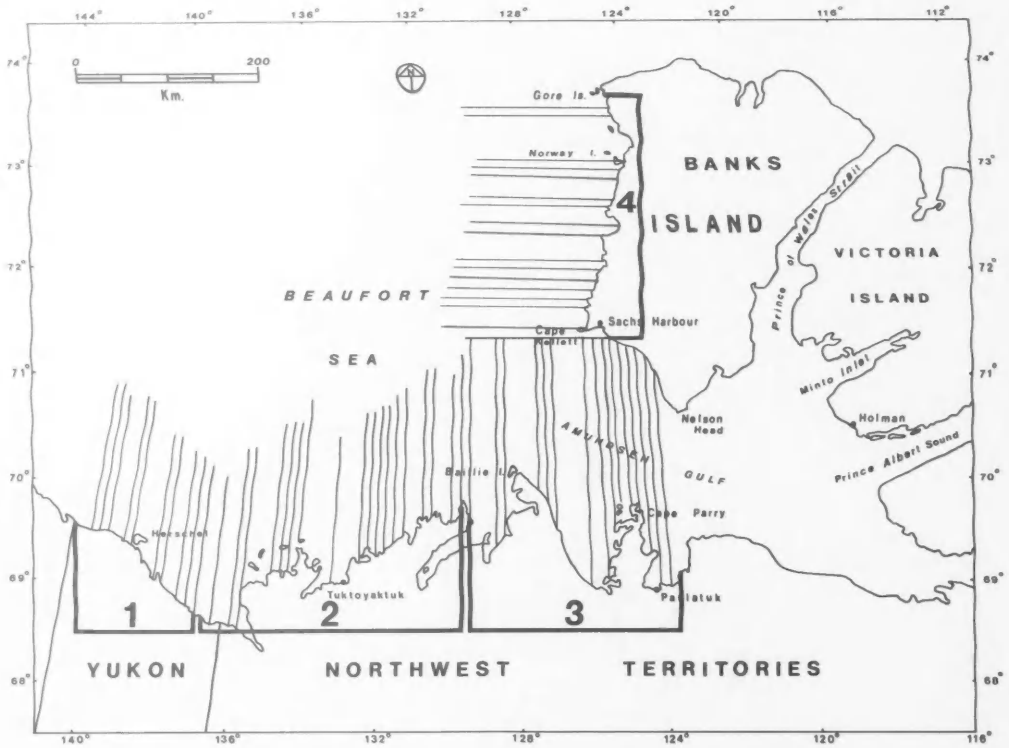

FIG. 1. Study area with the strata and the transect lines surveyed.

were hauled out on the ice, we planned our survey to coincide with the peak of the diurnal cycle during the molting period.

Because of the heterogeneous environment and limitations encountered in aerial surveying during the period of optimal haul out, we employed a stratified design to increase the precision of the estimates. The eastern Beaufort Sea was subdivided by a series of transects, 8 km apart drawn north from the mainland coast and west from Banks Island, offshore to a distance of 160 km. There was a total of 101 such transects. From our previous observations of seals in the study area, we suspected that their distribution and abundance in the sea-ice habitat was not uniform. Although we lacked detailed information on the parameters that caused those differences, we subjectively subdivided the transects into four mutually exclusive strata. The criteria for subdividing the strata were as follows: Stratum 1 was most affected by the inflow of freshwater from the Mackenzie River; stratum 2 was characterized each year by a series of east–west leads running parallel to the Tuktoyaktuk Peninsula, beginning at a depth of 20 m (Cooper 1974); stratum 3 was an extensive area of relatively unstable offshore ice; and, stratum 4 was a relatively stable ice area, although it also had a characteristic set of north–south leads running parallel to Banks Island and was usually the only area that sometimes remained heavily ice covered throughout the summer.

Because of budgetary limitations, not all transects could be surveyed. Sampling effort was allocated on a proportional basis with approximately 60% of the lines in each stratum selected at random. The number of transect lines flown in each stratum was 10, 18, 15, and 17, for stratums 1, 2, 3, and 4, respectively. Figure 1 shows the study area and the lines surveyed in each stratum.

The transects selected were flown at an altitude of 152 m (500 ft) at a speed of about 240 km/h (150 mph) in a Cessna 337 with two observers in the back seat, each counting on one side of the aircraft over strips from 0 to 0.2 km (0–⅛ mi) and from 0.2 to 0.4 km (⅛–¼ mi) wide. Strips were delineated using precalculated angles marked on the wing strut. Data recorded on each transect were partitioned at 2-min intervals to facilitate later analysis of a possible relationship between seal distribution and water depth. If a portion of the transect was ice free, it was deleted from the sample. Thus, only areas of potential habitat were surveyed. The percent of 2-min intervals in each stratum that were ice covered was taken to represent the proportion of ice cover in that stratum.

The side of the plane from which each set of

observations was made was recorded on all transects to facilitate testing for observer bias. For ringed seal counts, this was further subdivided into the inner and outer 0.2-km (⅛ mi) wide strips surveyed. Besides the ringed and bearded seals counted, all sightings of whales, polar bears, and unidentified seals were recorded.

The starting point for each transect was determined with the aid of a 1:250,000 map. A directional gyro was used to fly true headings and whenever possible, positions were checked with the Distant Early Warning (DEW) line sites.

In 1974 the transect lines were flown from June 15 to 29 and the survey was repeated from June 12 to 20, 1975.

Collection of Specimens in the Field

Ringed and bearded seals were collected from April to July 1974 and 1975 from offshore ice areas during the study. From each animal, standard length, axillary girth and blubber thicknesses on the neck, chest, and belly were measured and the reproductive tract, a tooth, and a toenail were collected. Reproductive material was examined fresh whenever possible and then preserved in AFA (alcohol–formalin–acetic acid). Stomach contents were also examined. Measurements and samples were also obtained from seals shot by Inuit hunters at Sachs Harbour, N.W.T., from June through August 1974 and 1975. Additional data were collected from seals killed by polar bears found in the course of continuing polar bear research in the western Arctic from October 1970 to August 1975.

Data Analyses

Population estimates — The population estimates for each stratum were obtained by multiplying the density by the number of square kilometres of suitable ice cover per stratum. Weighted linear regressions were used to calculate the average densities and confidence intervals for numbers of ringed and bearded seals per square kilometre of available habitat (Snedecor and Cochran 1967). The sample units for those analyses were the transects. This model assumes that the difference between the observed number of seals and the estimated number of seals increases linearly with area.

Models of distribution — In this analysis of distribution the total number of sampling units from the whole study area were combined. Each sample unit was the area surveyed from an airplane in a 2-min interval. Distribution for each species in each year was then tested against the Poisson and negative binomial models. Whenever the negative binomial model was found to fit a particular distribution, an estimate of the total seal population and the variance of this estimate were made (Seber 1973) and compared with estimates derived from the weighted linear regression model.

Observer and technique bias — To test for observer bias caused by differing abilities of each observer to see or identify the different species of seals, the means derived from the left half of the transects were tested against the means derived from the right half of the transects. To test for bias in identifying seals at different distances, the mean number of seals of each species counted in the inner quarters of each transect was tested against the mean number of seals counted in the outer quarters. A two sided t-test was used to check for observer and technique bias.

Distribution in Relation to Depth — Since the survey data were tallied in 2-min intervals on each transect, the count for each interval could be related to the corresponding average water depth. The density of seals per sampling unit was estimated for each specific depth category. Bathymetric maps were used to determine the average depth of water for each 2-min interval. If the seals were randomly distributed over depth, the expected number of seals would be solely a function of average density and the amount of area within each depth category. By comparing the expected and observed values, a chi-square test can be used to test the null hypothesis that ringed and bearded seals are randomly distributed over depth. A contingency table was generated to determine whether ringed and bearded seals had similar patterns of distribution.

Age determination — Canine teeth collected from the lower jaws of ringed seals (McLaren, 1958a) and the upper jaws of bearded seals (Benjaminsen 1973) were used for age determination. The teeth were placed in a buffered 25% formic acid solution for decalcification. Decalcification in buffered formic acid progresses gently, can be easily controlled, and does not damage the tooth if it remains in the acid too long. Dried teeth were decalcified in 7–10 days; teeth preserved in 10% formaldehyde took 15–20 days. The decalcification point was determined by checking for calcium ions in the formic acid solution.

Decalcified teeth were washed for 12–15 h in running tap water. Teeth stored prior to sectioning were placed in 70% ethanol. Teeth were soaked in water for at least 24 h immediately before sectioning for hydration of tissue and then imbedded in Lab-tech compound and cut on a cryostat at −10 to −20°C into longitudinal sections 10 μm thick.

Cut sections were placed in water pH 8–9 for at least 20 min before being affixed to a glass slide with egg albumen. Drying took 30–45 min at room temperature.

Sections were stained in a filtered 0.032% aqueous solution of Toluylene Blue (Allied Chemical, Morristown, N.J.). A more intense stain was obtained when the Toluylene Blue crystals were dissolved in alkaline water (pH 8–9).

Ages for ringed and bearded seals were determined by counting annuli in the cementum. Previous investigations (McLaren 1958a; Smith 1973a) used annuli in the dentine to determine the ages of ringed seals. McLaren (1958a) reported that this method was unreliable for some animals beyond 10 yr and for most beyond 20 because the annuli were highly compacted. The increase in thickness of the cementum is relatively constant, averaging 0.043 mm annually (Smith 1973a), and the corresponding annuli in the cementum were clear and easily read.

TABLE 1. 1974 calculations for ringed (RS) and bearded seal (BS) population estimates. Population of stratum = (density) (area) (proportion of area with ice cover); Total population = $\Sigma_{i=1}^{4}$ population of stratum; 95% CI = $\pm$ 1.96 $\sqrt{\Sigma_{i=1}^{4} (\text{SE}_i)^2 (\text{area}_i)^2 (\text{proportion with ice cover}_i)^2}$ of total population; Total population estimates: ringed seal: 41,983 $\pm$ 8,152; bearded seal: 2,757 $\pm$ 728.

	Density		SE				Population		±95% CI	
Strata	RS	BS	RS	BS	Area (km²)	Proportion ice cover	RS	BS	RS	BS
1	.5243	.0047	.0760	.0012	19,749	1.00	10,354	93	2,942	46
2	.4031	.0351	.0806	.0061	44,452	.91	16,306	1,420	6,390	484
3	.2873	.0185	.0500	.0043	39,992	.92	10,571	681	3,606	310
4	.1529	.0181	.0327	.0073	38,847	.80	4,752	563	1,992	445

TABLE 2. 1975 calculations for ringed (RS) and bearded seal (BS) population estimates. Total population estimates: ringed seal: 21,661 $\pm$ 4,919; bearded seal: 1,197 $\pm$ 239.

	Density		SE				Population		±95% CI	
Strata	RS	BS	RS	BS	Area (km²)	Proportion ice cover	RS	BS	RS	BS
1	.2108	.0127	.0469	.0024	19,749	.970	4,038	243	1,761	90
2	.1286	.0155	.0575	.0034	44,452	.633	3,619	436	3,171	188
3	.3602	.0120	.0546	.0016	39,992	.676	9,738	324	2,893	85
4	.4576	.0280	.0894	.0058	38,847	.240	4,266	194	1,634	79

Benjaminsen (1973) first reported that bearded seals could be aged by counting the annuli in the cementum of the upper canine tooth. Bearded seal teeth are poorly developed and wear rapidly so that most are worn down or missing by the 9th yr (Burns 1967). In cases where canine teeth were not available, the roots of any of the remaining teeth proved satisfactory for age determination.

Teeth collected from seals killed by polar bears were aged by decalcification, thin sectioning, and counting the annuli in the cementum. In some instances, only the claws of seals killed by polar bears remained at the site. These were cleaned in the laboratory, moistened on the surface, and the annual laminae counted (McLaren 1958a). This technique was adequate for young seals but only gave a minimum age for older animals.

Analysis of reproductive material — Female reproductive tracts were examined before fixation whenever possible. The fresh ovaries were hand sectioned with a scalpel, and the presence of a corpus luteum, corpus albicans of recent pregnancy, and follicular activity were recorded. Oviducts were flushed for eggs and the uterine horns were opened and examined for scars of recent pregnancy. Tracts were fixed and preserved in AFA for subsequent laboratory examination.

Results and Discussion

POPULATION ESTIMATES

Densities of ringed and bearded seals per stratum and population estimates for each species, in terms of the total number of seals hauled out on the ice in each stratum, indicate a significant decline in the numbers of ringed and bearded seals between 1974 and 1975 (declines of 48.4 and 56.6%, respectively) (Tables 1 and 2). The decline appeared to take place to varying degrees in different strata. For ringed seals, the greatest reduction in numbers occurred in strata 1 and 2 (61 and 78%, respectively), while numbers declined only slightly in strata 3 and 4 (8 and 10%, respectively) (Tables 1 and 2). Even though total numbers declined, the density of seals in strata 3 and 4 increased (by 25 and 199%, respectively), probably because there was considerably less ice so that molting seals were more concentrated on the remaining ice available. Similar increases in densities of Weddell seals (*Leptonychotes weddelli*, the ecological counterpart of the ringed seal in Antarctica) have been recorded in similar circumstances (Smith 1965; Stirling 1969). However, in strata 1 and 2, the density per unit of ice habitat declined significantly (60 and 68%, respectively), indicating that the drop in numbers could not be accounted for by local shift in concentration.

The significance of the differences in numbers and densities of bearded seals in the various strata between years is more difficult to interpret because the densities were much smaller than ringed seal densities and in general there is less known about bearded seals. However, the magnitude of the reductions in numbers recorded in the population estimates between years in

strata 2, 3, and 4 (69, 52, and 66%, respectively) must reflect real changes in absolute numbers. In strata 2 and 3 there was also a corresponding drop in density (56 and 34%, respectively). In stratum 4 there was a 35% increase in density, which, like ringed seals, probably occurred in response to the reduction in the proportion of ice cover. In stratum 1 the proportion of ice cover remained the same between years but the numbers and density of bearded seals increased markedly (265 and 63%, respectively). This may represent a partial change in distribution within the study area in response to the greater availability of sea-ice habitat in that stratum.

Other data also indicate a decline in the size of the seal populations. Ringed seals give birth to their single young in subnivean lairs in late March to early April. From 1972 to 1975 Smith and Stirling (1975 and unpublished data) quantitatively surveyed the same areas of sea ice habitat for ringed seal birth lairs in Amundsen Gulf. The density of ringed seal birth lairs dropped by as much as a factor of 10 between 1972 and 1973 and between 1974 and 1975 (Stirling and Smith 1977).

From 1972 to 1975, in comparable searches for polar bears in Amundsen Gulf, 265, 266, 63, and 57 sites were found where polar bears had dug out ringed seal lairs (Stirling and Smith 1977). A marked reduction in the numbers and productivity of ringed seals clearly took place in the eastern Beaufort Sea and Amundsen Gulf. The aerial surveys indicate that a similar decline in bearded seal numbers took place.

An approximation of the relative abundance of ringed seals to bearded seals in the study area was calculated by dividing the total number of ringed seals counted by the total number of bearded seals counted.

The mean value for the 2 yr was:

$$[(41{,}983/2{,}757) + (21{,}661/1{,}197)]/2 = 16.1.$$

Models of Distribution

Frequency counts for 1974 and 1975 ringed and bearded seal data (Table 3) did not agree with the Poisson model (ringed seals, $\chi_{74}^2 = 2634$, df = 6 and $\chi_{75}^2 = 1570$, df = 5; bearded seals $\chi_{74}^2 = 102$, df = 1 and $\chi_{75}^2 = 47$, df = 1). However, the observed bearded seal frequency distribution agreed closely with the negative binomial model (Bliss 1953) in 1974 ($\chi^2 = 1.573$, df = 2) and 1975 ($\chi^2 = 3.949$, df = 1). The fact that the two κ values were significantly different suggests that yearly changes in the habitat affect the distribution of bearded seals (1974 $\kappa = 0.1244$; 1975 $\kappa = 0.0704$). The ringed seal data were only found to fit in 1975 ($\chi_{75}^2 = 12.4$, df = 10). The κ statistic was estimated as 0.2319. Comparing this κ value with the bearded seal κ value for 1975 suggests a significant difference in distribution between the two species, with bearded seals being more clumped in distribution than ringed seals.

The negative binomial model can be useful in increasing the precision of the population estimates (Table 4). The coefficient of variation for the population estimate is:

$$[C(\hat{N})] = \sqrt{\frac{V[\hat{N}]}{\hat{N}^2}} = \sqrt{\frac{1}{n}\left(\frac{A}{a\hat{N}} + \frac{1}{\kappa}\right)}$$

where C = coefficient of variation, $\hat{N}$ = natural estimate of total population, n = number of sample plots, A = area occupied by the population, V = variance of seals per sample unit,

TABLE 3. 1974 and 1975 ringed and bearded seal observations tabulated by number of seals per sample unit.

Class (no. seals/sample unit)	Ringed seals		Bearded seals	
	1974	1975	1974	1975
0	508	439	956	688
1	169	80	59	36
2	105	58	22	10
3	79	33	6	2
4	38	33	6	0
5	32	25	0	0
6	23	15	2	0
7	12	13	0	0
8	20	5	0	0
9	14	5	0	1
10	4	4	0	0
11	5	5	0	0
12	4	2	0	0
13	3	4	0	0
14	5	4	0	0
15	1	1	0	0
16	3	2	0	0
17	2	2	0	0
18	0	0	0	0
19	2	0	0	0
20–36	22	7	0	0
Total	1051	737	1051	737

TABLE 4. Comparison of the variance estimates derived from negative binomial and linear regression models. SE_{NB} = standard error of negative binomial; SE_{LR} = standard error of linear regression.

Year	Seal species	κ Value	SE_{NB}	SE_{LR}
1974	bearded	.1244	343	371
1975	bearded	.0704	255	122
1975	ringed	.2319	1849	2510

TABLE 5. Bias calculations between observers for 1974 and 1975 ringed and bearded seal distributions. *Significant at the 95% level.

	1974				1975			
Strata	Left mean	Right mean	df	t value	Left mean	Right mean	df	t value
				Ringed seal				
1	1.695	1.022	10	1.770	.511	.581	10	−.39
2	1.170	.918	17	.754	.256	.410	17	−.63
3	.766	.722	13	.224	1.050	.816	13	1.07
4	.377	.415	17	−.234	1.175	1.195	17	−.05
				Bearded seal				
1	0.0	.024	10	−4.000*	.033	.033	10	0.0
2	.061	.120	17	−1.680	.060	.021	17	1.22
3	.039	.058	13	−.833	.023	.038	13	−.84
4	.047	.047	17	0.0	.069	.039	17	.86

TABLE 6. Bias calculations between the inner and outer means of ringed seal observations for 1974 and 1975. *Significant at the 95% level.

	1974				1975			
Strata	Inner mean	Outer mean	df	t value	Inner mean	Outer mean	df	t value
1	.994	1.723	10	−2.08	.40	.693	10	−1.40
2	.617	1.471	17	−2.58*	.287	.379	17	−.41
3	.537	.951	13	−1.96	.906	.959	13	−.24
4	.238	.553	17	−1.86	.960	1.410	17	−1.23

κ = dispersion parameter of the negative binomial.

This equation shows that as κ or $\hat{N}$ gets larger, the relative precision of the estimate is increased. One problem with this technique is that it assumes that the distributional pattern of seals fits the negative binomial. Pielou (1969) indicates that it is not legitimate to both confirm the distribution and estimate the population size with the same data. Therefore, a stratified design incorporating a weighted linear regression model is most efficient and effective for estimating populations of ringed and bearded seals.

OBSERVER BIAS

Observer bias was only significant in the bearded seal observations in stratum 1 in 1974 (Table 5; $t = -4.0$, df = 10). However, as only six bearded seals were seen altogether in that stratum, the difference may simply have resulted from inadequate sample size and the tendency for bearded seals to aggregate. Thus, we concluded that there was no significant observer bias, in either the ability to see or identify seals, between the left and right sides of the transects.

The only significant difference between the mean number of ringed seals observed in the inner and outer quarters of each transect occurred in stratum 2 in 1974 (Table 6). However, the signs of all the t statistics were negative. If it is assumed that for each of the eight comparisons that the inner mean equals the outer mean, then the probability of observing χ negative differences between the inner and outer means would have a binomial distribution with $\rho = 0.5$ and $\eta = 8.0$. Thus, the probability of observing eight negative differences ($\chi = 8$) is approximately 0.004. This suggests that the mean of the outer 0.2 km of the transect was significantly different from the inner mean.

It is not clear why the number of ringed seals counted in the outer half of the transect was consistently higher than the number counted on the inner half. One possibility is that when an observer is flying at 152 m (500 ft) at a ground speed of 240–320 km/h (150–200 mph), it may subconsciously be less strain on his eyes to look out farther. A slower survey speed would not resolve the problem because many of the seals would go into the water before the plane was over them, so that they would not be observed.

TABLE 7. Distribution vs. depth calculations for 1974 and 1975 ringed seal (R) and bearded seal (B) observations.

Depth (m)	1974 No. km² of *i*th depth	1974 Observed no. R	1974 Observed no. B	1974 Expected no. R	1974 Expected no. B	1975 No. km² of *i*th depth	1975 Observed no. R	1975 Observed no. B	1975 Expected no. R	1975 Expected no. B
0–25	1761	472	19	582	39	1547	455	19	434	22
26–50	1518	619	79	501	33	841	210	20	240	12
51–75	679	235	21	224	15	360	50	9	101	5
76–100	311	63	6	103	7	197	28	1	52	3
101–150	632	212	8	209	14	378	176	4	106	5
151–200	461	105	12	152	10	234	84	0	66	3
201–300	642	239	4	212	14	288	103	6	81	4
301–400	451	88	3	149	10	182	27	0	51	3
401–500	65	59	1	21	2	62	8	1	17	1
501–1000	197	63	0	65	4	172	35	2	48	2
>1000	238	142	0	79	5	124	55	0	35	2
			1		11			14		23
	$\chi^2_{R^{74}} = 226.69$		$\chi^2_{B^{74}} = 101.03$			$\chi^2_{R^{75}} = 130.25$		$\chi^2_{B^{73}} = 12.46$		
	$\chi^2_{.05,10} = 18.3$		$\chi^2_{.05,8} = 15.5$			$\chi^2_{.05,10} = 18.3$		$\chi^2_{.05,10} = 7.8$		

TABLE 8. Distribution vs. ice-type calculations for 1974 and 1975 ringed and bearded seal observations.

Class	Proportion of ice coverage in oktas[c]	No. km² ice 1974	No. km² ice 1975	1974 Observed no.[a] RS	1974 Observed no.[a] BS	1974 Expected no. RS	1974 Expected no. BS	1975 Observed no.[b] RS	1975 Observed no.[b] BS	1975 Expected no. RS	1975 Expected no. BS
1	0–2	414	1177	3	3	128	8	35	9	302	16
2	3–4	172	267	12	0	53	4	8	4	68	3
3	5–6	478	169	66	1	148	10	0	0	43	2
4	7–8	6430	3082	2241	151	1993	133	1160	49	790	41
Total		7494	4695	2322	155	2322	155	1203	62	1203	62

[a]1974: χ^2RS = 230, χ^2BS = 17.7: [b]1975; χ^2RS = 505, χ^2BS = 7.0; $\chi^2_{.05,3} = 7.82$. [c]1 okta = $\frac{1}{8}$ coverage.

The difficulty most likely occurs in the observer's looking straight down to observe the innermost portion of the inner half of each side of the transect. One possible solution might be to precalculate the observer's viewing angles so that the transects are transposed slightly farther out, thus making it more comfortable to scan the whole area continuously. Also, even at this height and speed, more seals may be frightened into the water on the inner portion of the transect before being counted, than on the outer portion.

ANALYSES OF DISTRIBUTION

A comparison of the proportions of ringed and bearded seals expected and observed in relation to depth showed that neither species was distributed randomly (Table 7). In addition, for bearded seals the consistency with which the observed values were larger than the expected values for depths 25–75 m, and vice versa for depths > 75 m, indicates a preference for shallower water.

Comparisons between the patterns of distribution in relation to depth of ringed and bearded seals were derived from a contingency table generated from the observed values in Table 7. For both years the χ^2 values were significantly different (1974: $\chi^2 = 70.44$, df = 10; 1975: $\chi^2 = 10.7$, df = 3), which suggests that ringed and bearded seals were not distributed over depth in the same manner.

A comparison of the proportions of ringed seals expected and observed in relation to percent ice coverage showed that the distribution of the seals was not random (Table 8). In 1974 and 1975, fewer seals were observed than were expected in the first two classes, and conversely in the second two classes, indicating that ringed seals prefer areas with a high percentage of ice coverage. For the bearded seal the results are not as clear. In 1974 they showed a preference for

TABLE 9. Proportions (and frequencies) of pup, adolescent (Adoles.) and adult ringed seals collected in the offshore waters of the eastern Beaufort Sea and Amundsen Gulf; data from two other studies in the eastern arctic and from seals killed by polar bears in the Beaufort Sea and Amundsen Gulf are also included.

	Eastern Beaufort Sea and Amundsen Gulf				Eastern arctic				Polar bear killed seals	
					McLaren (1958a)		Smith (1973a)			
Age class	1966 (*N*)	1972 (*N*)	1974 (*N*)	1975 (*N*)	Offshore[a] (*N*)	Inshore[a] (*N*)	Inshore[b] (*N*)	Inshore[b] (*N*)	1971–73 (*N*)	1974–75 (*N*)
Pups	.08(15)	.44(128)	.00(0)	.02(4)	.16(17)	.13(57)	.31(896)	.32(857)	.50(17)	.00(0)
Adoles. (1–6 yr)	.20(39)	.30(87)	.39(25)	.24(45)	.63(67)	.58(262)	.36(1046)	.55(1447)	.29(10)	.09(5)
Adults	.72(136)	.26(78)	.61(40)	.74(136)	.21(23)	.29(135)	.33(954)	.13(338)	.12(4)	.53(30)
Unclassified	—	—	—	—	—	—	—	—	.09(3)	.38(22)

[a]Collections actually made from 1951 to 1955.
[b]Collections actually made in 1966, 1967 and 1970.

TABLE 10. Ovulation rate and the proportion of sexually mature ringed seals[a] and bearded seals[b] with a corpus albicans (CA) of recent pregnancy collected in the eastern Beaufort Sea. The samples from 1974 and 1975 include seals with mature follicles collected immediately before ovulation. Comparative data on the rate of ovulation from four other studies are included.

	Ringed seal			Bearded seal		
Year collected	Sample size	Ovulation rate	% seals with CA of recent pregnancy	Sample size	Ovulation rate	% seals with CA of recent pregnancy
1972	27	.74	.44			
1974	23	.39	.00	9	1.0	.56
1975	80	.49	.01	24	.46	.33
Smith (1973a)	538	.92				
McLaren (1958a)		.78				
Johnson et al. (1966)	280	.94				
Burns (1967)				133	.83	

[a]Includes all females greater than 6 yr (McLaren 1958a).
[b]Includes all females greater than 5 yr (Burns 1967).

areas of higher ice cover, while in 1975 their distribution in relation to the degree of ice cover was not significantly different from random.

AGE STRUCTURE

The sample sizes were too small and the number of age-classes too numerous to warrant detailed presentations in an age-frequency table. Table 9 gives the proportion of pups, adolescents (1–5 yr), and adults in samples of ringed seals collected throughout the offshore areas of the eastern Beaufort Sea and Amundsen Gulf as well as from three other areas and of seals found killed by polar bears. The sample sizes of bearded seals collected in the study area and killed by polar bears gave similar results but the sample sizes were too small to merit inclusion.

Smith and Stirling (1975 and unpublished data) documented a marked reduction in ringed seal productivity in 1974 and 1975 in comparison with 1972 and 1973. Pups were almost totally absent either in our collections or in the age structure of the seals killed by polar bears.

Reproductive Data

The ovulation rates and the presence of a corpus albicans of recent pregnancy for ringed seals in our samples from 1974 and 1975 were roughly half those recorded in comparative collections (Table 10). Presumably the fact that as a group the ringed seals were in a poorer physical condition (Smith and Geraci 1975) was responsible for the lowered ovulation rates. It is not clear whether adult females that ovulated did not copulate, did not conceive, or experienced intrauterine mortality. However, reproductive tracts of 4 of the 130 adult female ringed seals we examined showed evidence of the pregnancy having been terminated sometime before the normal period of parturition or of loss of the pup near the time of birth in late March to early April. Three females had uterine scars that had not completely healed but they were not lactating and had regressing corpora albicantia; one had a partially resorbed fetus in the uterine horn. Although the sample sizes from adult bearded seals in 1974 and 1975 were small, they also indicated a reduction in reproductive activity.

Ecological Considerations

In 1974 and 1975 a major decline took place in the numbers and productivity of ringed and bearded seals in the eastern Beaufort Sea. Although the decrease in numbers did not take place equally in all strata, the overall decline could not be explained simply by local shifts in distribution. Even if the productivity of ringed seals in 1974 was zero, the decrease in the total population estimates (48.2%) could not be approximated by using a published overall mortality estimate of 15% (Smith 1973a). No similar crude mortality estimates exist for bearded seals but the magnitude of the reduction in the population estimates (56.6%) could not be accounted for by that factor alone.

There could be two explanations for the reduction of numbers, extensive mortality combined with reduced productivity or large-scale emigration. Smith and Geraci (1975) suggested that ringed seals were in poorer nutritional condition in 1974 than in previous years. Correspondingly, there were marked reductions in productivity of young, in general reproductive activity, and in the proportions of young in the population of ringed seals observed (Smith and Geraci 1975; Smith and Stirling 1975; and this study). Higher age-specific mortality of younger age-classes could not be demonstrated specifically, but the virtual absence of young of the year in 1974 and 1975 and reduction in the proportions of subadults in the samples of ringed seals from 1974 and 1975 could have been influenced by that factor.

Stirling and Smith (1977) speculated briefly on the possibility of large-scale movements and there is some evidence that it occurred. Smith (1976a) recorded movements of branded ringed seals from eastern Beaufort Sea, to Point Barrow, Alaska, and to Icy Cape in Siberia. In 1975 J. J. Burns (Alaska Department Fish and Game, Fairbanks, personal communication) repeated his earlier seal surveys (Burns and Harbo 1972) of the north coast of Alaska and recorded significant decreases in the numbers of seals, similar to those reported here, but he also recorded a severalfold increase in the numbers and densities of seals to the west in the Chuckchee Sea.

The mechanism for large-scale facultative movements may already exist. Each autumn there is a westward migration of subadult ringed seals from the eastern Beaufort Sea which has long been known to the Inuit of the region. The magnitude of this emigration from the Beaufort Sea, and the extent to which immigration occurred, could vary significantly with ecological conditions between years. The main difficulty with the large-scale movement hypothesis is that presumably any available ringed seal habitat is already occupied to its carrying capacity, which would seem to preclude successful invasion by large numbers of immigrants.

We are not certain what caused these changes, but the only major factor that was markedly different, that we are aware of, was the condition of the sea ice. In the winter of 1973–74 the winter winds blew predominantly from the northwest instead of alternating between the southeast and northwest as they usually do. Consequently, instead of formation of the usual series of leads that open and refreeze parallel to the mainland coast and west coast of Banks Island, beginning at about the 20-m depth contour (Cooper 1974), the sea ice was heavily compacted and frozen solid against the land and for many kilometres offshore.

Subjectively, it also appeared that in 1974 and 1975 there was less snow cover in which ringed seals could construct their subnivean birth lairs compared with 1972 or 1973 when there was much more snow cover and productivity was high (Smith and Stirling 1975 and unpublished data). However, this factor may have been less important, since bearded seals, which give birth to their young on the exposed sea ice, showed a decline in numbers similar to that of the ringed seals.

The changes in sea-ice conditions could have

affected the seals in two ways. Firstly, it may simply have been more difficult for the large numbers of bearded and ringed seals that normally concentrate along those lead systems to maintain their breathing holes through the winter. Although we know that under normal conditions, ringed and bearded seals can maintain their breathing holes in refreezing ice by abrading it with the heavy nails of their foreflippers, we do not know if they can continue to maintain their breathing holes in heavy pressure ice if it continues to move and compact. Secondly, it is possible that in the winter of 1973–74 when the ice was thicker and there were fewer open leads through the spring, less sunlight penetrated into the sea, resulting in a significant reduction in the level of primary production. Grainger (1975) reported that thicker ice or heavier snow cover could significantly depress primary productivity. Grainger also noted that the Beaufort Sea supported, at best, a fairly low rate of primary and secondary production and a relatively uncomplicated food chain, so that changes at the lower levels could have rapid and significant effects on species in the upper trophic levels.

If there was a significant reduction in the availability of food for seals, one would predict that they might be in poorer condition, have lower productivity and higher mortality rates, and possibly emigrate. There is some evidence for all these consequences. Furthermore, in 1966, following on the abnormally heavy ice conditions of 1964, only 8% of a sample of 190 seals taken at Sachs Harbour were young of the year (Table 9), suggesting that the changes we have documented in this paper may have occurred in the same manner before.

The decline in the numbers of seals in the eastern Beaufort Sea also had a marked effect on the polar bears that prey and scavenge upon them. Primarily, there were fewer seals available to be preyed upon. In 1974, as a result of the greater compression, the ice cover was thicker and rougher so that on the average, the seals present were probably less accessible to the bears because of the amount of ice over their breathing holes, which resulted in a lower predation rate. In 1974 hardly any seals killed by polar bears were found, probably because fewer were killed, and consequently more of each carcass was consumed, making it easier for the remains to be hidden by drifting snow.

Stirling et al. (1976) pooled data collected from polar bears in the eastern Beaufort Sea 1971–73 and compared those data with pooled data from 1974–75. The natality of 5-yr-old females (age of first breeding for most female polar bears), and of 6–18-yr-old females dropped by $> 50\%$. The percent of adult females captured that were accompanied by cubs of any age dropped from 82.2% (37/45) to 54.7% (35/64). Estimates of the size of the polar bear population of the western arctic indicated a decline as well.

Concurrent with the polar bear mark-and-recapture program in the western arctic from 1971 through 1975, similar programs were conducted to the west in Alaska and to the northeast. Only eight bears were recaptured out of the study area, and of these, seven were captured in 1975. Five of these were adults and two of the three subadults were the offspring of one of the adults. Stirling et al. (1975) suggested that this movement of bears, especially by dominant adults, was related to the sudden decline in numbers of seals.

Large numbers of arctic foxes survive during the winter by scavenging on the remains of seals killed by polar bears. In addition, foxes may also prey heavily on newborn ringed seals in their birth lairs, although the extent to which this occurs may vary greatly between years (Smith 1976b). The lowered amount of carrion and fewer seal pups available for predation in 1973–74 resulted in markedly less food for the arctic foxes. As a result, the foxes probably traveled more in search of food and came into more contact with traps resulting in the highest catch for several years. Arctic foxes tagged on Banks Island in the winter of 1973–74 were recaptured in Alaska and on the west coast of Hudson Bay during the following year (R. D. Hennig, Beak Consultants, Calgary, personal communication). The harvest of arctic foxes in 1974–75 was half that of the previous year, apparently in response to the lowered food supply for overwintering foxes and possibly because of emigration as well.

Management of marine mammals in polar regions appears to be based on the a priori assumption that the ecosystem is stable, since quotas, once established, appear to remain fixed. However, Dunbar (1968) noted that because of the evolutionary youth of the polar marine ecosystems and the paucity of species involved, they are prone to large fluctuations in productivity and biomass, and even the possibility of local extinctions. In this study we have demonstrated large-scale changes in the distribution and abundance of seals and their consequent effects on polar bears and arctic foxes. Clearly, we need to study the speed with which the various com-

ponents of the arctic marine ecosystem can respond to such large-scale natural changes to enable management practices to respond effectively. Quotas that were safe for a healthy population could be devastating to a reduced population with lowered productivity. In addition, it will be essential to understand more about the causes, magnitude, and speed of such fluctuations to be able to predict the variable degree to which the detrimental aspects of activities such as offshore drilling and eventual production of petrochemicals or the dumping of mine tailings could affect the ecosystem.

Acknowledgments

We are particularly grateful to the following organizations for logistic support: Canadian Wildlife Service, Polar Continental Shelf Project, and the Beaufort Sea Project. We thank the following individuals for their invaluable assistance in the field: D. Andriashek, G. Beyersbergen, Wendy Calvert, D. Cameron, W. Hoffman, J. Langevin, D. Larson, and P. Latour; T. G. Smith for age determination of the 1972 Sachs Harbour seal collection; P. Archibald, W. Calvert, and G. Parker for their assistance in the laboratory; Dr. D. B. Siniff for statistical advice in the design of the aerial survey and M. Kingsley for assistance with statistical analysis; P. Smith for constructive criticism and editing of the manuscript; and Corporal B. Gudmundson, RCMP Sachs Harbour, for assistance and hospitality. We received a great deal of advice, assistance, and information from the following Inuit of the western arctic: A. Carpenter, Angus Elias, Albert Elias, P. Esau, E. Esau, J. Kevik, W. Lucas, J. Lucas, D. Nasogaluak, H. Nasogaluak and F. Sidney.

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Growth Model for Alaska King Crab (*Paralithodes camtschatica*)

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MCCAUGHRAN, D. A., AND G. C. POWELL. 1977. Growth model for Alaska king crab (*Paralithodes camtschatica*). J. Fish. Res. Board Can. 34: 989–995.

A stochastic growth model is presented to represent the growth in carapace length of the Alaska king crab (*Paralithodes camtschatica* Tilesius). Two submodels are combined to yield the growth model: (1) growth increment as a function of premolt length and molting history and (2) a probabilistic model of frequency of molting by age, premolt length, and molting history. The results of a computer simulation of the growth model are presented. Frequency of ages at various lengths and frequency of lengths at each age are given. Frequency of molting during early life was found to greatly influence growth rate.

Key words: king crab, growth, length, stochastic model growth increment, molting, growth model

MCCAUGHRAN, D. A., AND G. POWELL. 1977. Growth model for Alaska king crab (*Paralithodes camtshatica*). J. Fish. Res. Board Can. 34: 989–995.

Nous présentons un modèle de croissance stochastique représentant la croissance en longueur de carapace du crabe royal d'Alaska (*Paralithodes camtschatica* Tilesius). Deux sous-modèles sont combinés pour donner le modèle de croissance: (1) l'augmentation de croissance comme fonction de la longueur avant la mue et de l'historique des mues, et (2) modèle probabiliste de la fréquence des mues par âge, de la longueur avant la mue et de l'historique des mues. Nous donnons les résultats d'une simulation sur ordinateur du modèle de croissance. Nous indiquons la fréquence des âges à diverses longueurs et la fréquence des longueurs à chaque âge. Nous constatons que la fréquence des mues au début de la vie affecte grandement le rythme de croissance.

Received October 14, 1975
Accepted March 16, 1977

Reçu le 14 octobre 1975
Accepté le 16 mars 1977

MATHEMATICAL models for animal growth are generally univariate functions of time. They are most often based upon a differential equation expressing the rate of change in size as a function of size. Models of this type have been used with considerable success for predicting size at age for individuals that grow continuously or for the average size at age for populations of continuously growing individuals. Two problems are encountered when these classical models are used to describe the growth of Crustacea. Crustaceans do not grow in length continuously; they increase only at ecdysis, and the large variability of size at age is not described by an average growth function for the population. A different approach was taken in developing a mathematical model to describe the growth in the Alaska king crab (*Paralithodes camtschatica* Tilesius).

There are two aspects to crustacean growth that must be modeled: the frequency of molting and the magnitude of the growth increment at each molt. The two aspects combined yield a growth model. Carapace length has been used as the measure of growth, since width and weight are functions of length and a large data set on king crab lengths was available. We hope that this model will be of use in describing growth in length and estimating the variability in lengths at different ages.

The data from which growth was described and parameters were estimated originated from tag-and-recapture studies in the Kodiak area conducted by the Alaska Department of Fish and Game, National Marine Fisheries Service (previously U.S. Bureau of Commercial Fisheries); studies on penned crabs at Kodiak, Alaska, conducted by the Alaska Department of Fish and Game (Gray 1963; Powell 1967); and studies on immature crabs by Weber (1965). The numbers of tag recoveries used in parameter estimation with each of the several different molt-history groups are presented in Table 1. These data were used primarily to obtain insight into the form of

Printed in Canada (J4023)
Imprimé au Canada (J4023)

TABLE 1. Tag recoveries used for parameter estimation, Kodiak area. Most recoveries are used several times, e.g. MMM are also MM.

Molt seasons free	Explanation of symbol	Symbol	No.	Explanation of symbol	Symbol	No.
1	Molted in recovery year, and the year previous	MM	2861	Molted in recovery year and skip-molted the year previous	MS	469
1	Failed to molt in recovery year, molted the previous year	SM	5668	Failed to molt in recovery year skip-molted the year previous	SS	580
2	Molted in recovery year, and molted each of the 2 previous yr	MMM	53	Molted in recovery year, skip-molted the year previous and molted 2 yr previous	MSM	383
2	Failed to molt in recovery year, molted each of the 2 yr previous	SMM	420	Failed to molt in recovery year, skip-molted the year previous and molted 2 yr previous	SSM	110
2	Molted in recovery year, molted the year previous and skip-molted 2 yr previous	MMS	2	Molted in recovery year, skip-molted each of the 2 yr previous	MSS	48
2	Failed to molt in recovery year, molted the year previous and a skip-molt 2 yr previous	SMS	76	Failed to molt in recovery year, skip-molted each of the 2 previous years	SSS	1

growth functional relationships and to develop a growth in length model for the Kodiak area.

Growth per Molt

There is considerable information on length increment for king crabs for particular premolt lengths and shell ages. Powell (1967) presents length increments for the Kodiak area. Weber and Miyahara (1962) give length increments for large crabs of the eastern Bering Sea and Weber (1965) presents increment values for immature king crabs of the southeastern Bering Sea.

Since there is no method for obtaining the age of large crabs, data are not available for determining the relationship between increment size and age. Without information on growth per molt at different ages, a realistic growth model is difficult to construct. One can, however, make certain assumptions concerning age that will lead to a model for describing growth reasonably well.

Let X_{L_i} be a normal random variable modeling the length increment at premolt length L_i.

$$X_{L_i} \sim N[f(L_i), \sigma^2_{L_i}]$$

where f_{L_i} is the expected length increment for premolt length L_i, and $\sigma_{L_i}{}^2$ is the variance of X_{L_i}.

$$L_0 = 2.5 \text{ mm and } L_i = \sum_{j=1}^{i-1} X_{L_j} + L_0$$

where $i = 2, 3, \ldots,$ and L_0 is the average length in millimetres of the first adult form.

From tagging studies, observations on penned crabs, and observations by Weber (1965), we have a set of observations (L_i, X_{L_i}), but unfortunalety we do not know the value of i, i.e. we have premolt size and growth increment, but we do not know how many molts have previously occurred.

An empirical model for average length increment as a function of premolt length was developed by examining the data set (L_i, X_{L_i}). Length increment data for males were averaged in 5-mm premolt length-classes and by molt history (Table 2). Molt history for males was determined from multiple recaptures and shell condition at time of tagging. Individual observations for males and females are presented in Fig. 1 and 2. Analysis of the data in Table 2 yields the following relationship for crabs over 120 mm:

$$f_{\delta}(L_i, \text{MSS}) < f_{\delta}(L_i, \text{MSM}) < f_{\delta}(L_i, \text{MMS}) < f_{\delta}(L_i, \text{MMM})$$

Although only two data points were available for

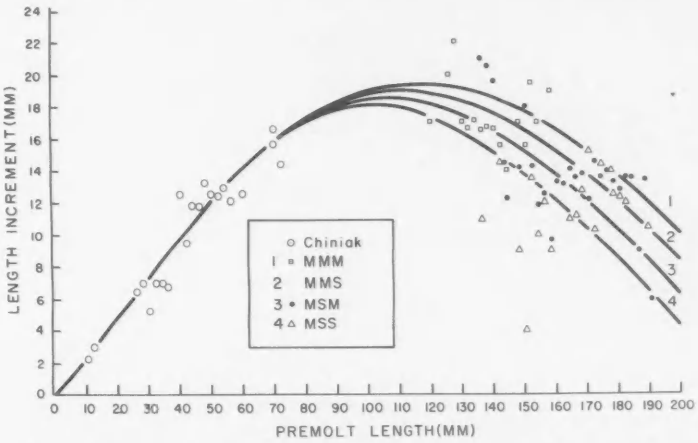

FIG. 1. Carapace length increment (millimetres) as a function of premolt length (millimetres) and the previous 2 yr of molting history for male king crabs.

TABLE 2. Mean carapace length increment for male king crabs of different premolt lengths and molting history.

Premolt length class (mm)	Molt history			
	MMM $\bar{X}(n)$	MSM $\bar{X}(n)$	MSS $\bar{X}(n)$	MMS $\bar{X}(n)$
120–125	17.0(1)			
125–130	21.0(2)			
130–135	18.3(12)			
135–140	16.8(12)	18.3(4)	11.0(1)	15.0(2)
140–145	15.2(11)	13.4(14)	17.0(3)	
145–150	16.0(5)	12.6(28)	9.0(1)	
150–155	17.0(6)	11.6(32)	10.3(6)	
155–160	16.5(4)	11.5(49)	10.3(3)	
160–165		12.7(52)	11.9(16)	
165–170		13.0(46)	12.7(7)	
170–175		13.5(48)	13.0(5)	
175–180		13.7(58)	11.7(6)	
180–185		13.9(38)		
185–190		11.6(10)		
190–195		11.5(4)		

the MMS molt group, it was placed in the above relationship because the length increments of the other three groups suggest that if a crab molted the previous year, its length increment upon molting in the current year will be higher on the average.

Mean length increment for crabs of both sexes under 60 mm premolt length is modeled as a linear function of premolt length. At approximately 60 mm the average rate of change in the length increment at each molt begins to decline and reaches zero at approximately 70 mm premolt length for females and 120 mm premolt length for males. Decrease in the rate of change of length increment occurs before the onset of female sexual maturity; perhaps the decrease can be explained for females by a shifting of energy away from growth and into reproduction.

The data for both sexes suggest a relationship for mean growth increment as a function of premolt length of the form:

$$f(L_i) = \begin{cases} bL_i & \text{for } 2.5 \text{ mm} < L_i \le 60 \text{ mm} \\ C_1 \left\{ \exp\left(\dfrac{-|L_i - C_2|^{C_4}}{C_3} \right) \right\} & \text{for } L_i > 60 \text{ mm} \end{cases}$$

The curves were forced to match the linear function at 60 mm and give an adequate fit to the sample means in Table 2. Parameters for MMM, MSM, and MSS were fitted by least squares. Since the length increment for crabs decreases with skip-molting frequency, the model for MMS molt sequence was fitted between MMM and MSM. The models are shown graphically in Fig. 1 and 2 with individual data points. The functions for mean length increment are:

$$f_{\varphi}(L_i) = \begin{cases} 0.24L_i & \text{for } 2.5 < L_i \le 60 \text{ mm} \\ 14.97 \exp - \left\{ \dfrac{|L_i - 70|^{1.7}}{1300} \right\} & \text{for } L_i > 60 \text{ mm} \end{cases}$$

$$f_{\delta}(L_i \ldots) = \left\{ \begin{array}{ll} 0.24L_i & \\ 19.45 \exp \left\{ -\dfrac{(L_i - 117.5)^2}{11000} \right\} & \text{for (MMM)} \\ 18.97 \exp \left\{ -\dfrac{(L_i - 112.5)^2}{10000} \right\} & \text{for (MMS)} \\ 18.51 \exp \left\{ -\dfrac{(L_i - 107.5)^2}{9000} \right\} & \text{for (MSM)} \\ 18.05 \exp \left\{ -\dfrac{(L_i - 102.5)^2}{8000} \right\} & \text{for (MSS)} \end{array} \right\} \begin{array}{l} 2.5 < L_i \le 60 \text{ mm} \\ L_i > 60 \text{ mm} \end{array}$$

The differences in mean length increment of crabs with similar premolt length but having

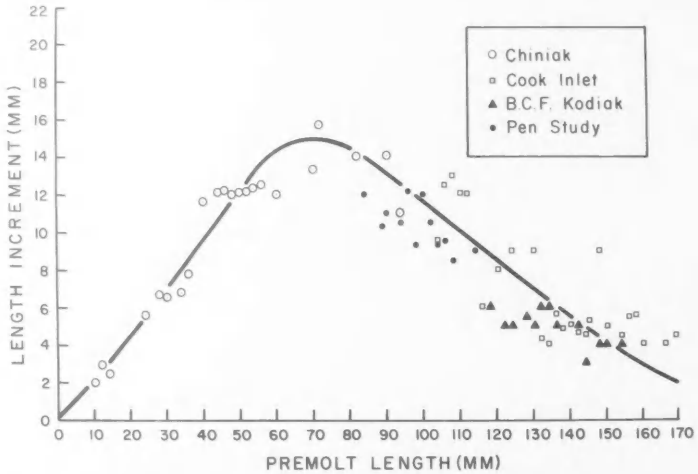

FIG. 2. Carapace length increment (millimetres) as a function of premolt length (millimetres) for female king crabs.

different molt histories cannot be explained with the present information available.

The variance of X_{L_i} appears to increase linearly with L_i. For the Kodiak population, the model used was:

$$\text{var}\ (X_{L_i}) = 0.042L_i - 0.104$$

Weber and Miyahara (1962) fitted a linear equation to length increment data over the range of 100–170 premolt lengths. They indicate that a second degree polynomial gave a better fit to their data. If they had included data on smaller and larger crabs, the curvilinear relationship between increment and premolt would have been clear.

Frequency of Molting

There is little information available concerning the annual frequency of molting in immature crabs. Powell (1967) claims postlarval crabs of both sexes molt 7 or 8 times the 1st yr, 4 or 5 times the 2nd yr, 2 or 3 times the 3rd yr, and 1 or 2 times the fourth year. After attaining sexual maturity in the 4th or 5th year, adult males molt annually for several years and then some individuals begin to skip-molt at approximately 7 yr of age, becoming biennial and triennial molters. In female crabs molting is correlated with reproduction. Molting occurs just before mating each year; hence, females after 5 yr of age are considered annual molters. Powell's description of the molting pattern is based on determining approximate age in younger crabs by length-frequency observations. The exact molting patterns for older crabs are not known exactly, but the patterns adopted for this model are considered the most likely to occur in light of present knowledge.

Data from the various tagging studies yield estimates of the probability of molting, given premolt length and molting history. Logistic functions were used to model this phenomenon. Figure 3 shows the functions with parameters estimated from the Kodiak data. Insufficient data were available to estimate a function for the probability of molting for crabs that in the previous two molting seasons had skip-molted and molted in that order (MMS and SMS crabs), so a function was constructed that seemed reasonable based on the small amount of information available. The probability function, P (molting | molted or

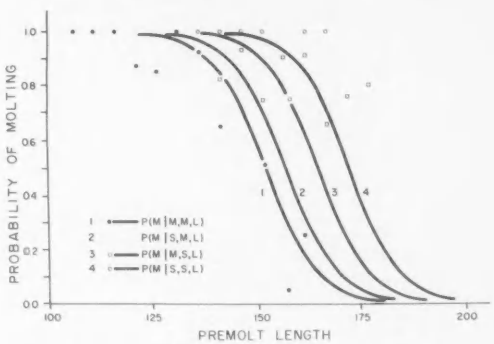

FIG. 3. The conditional probability of molting given premolt length and the previous 2 yr of molting history for male king crabs.

skipped 2 yr ago, molted or skipped last year); is:

$$\frac{1}{1 + e^{-(25.0-0.17(L_i-a))}}$$

Estimated parameters for the Kodiak populations are:

	Molt sequence	Probability	Parameter
1	MMM	$P(M\|M, M, L_1)$,	$a = 2.5$
2	MSM	$P(M\|M, S, L_i)$,	$a = 7.5$
3	MMS	$P(M\|S, M, L_i)$,	$a = 17.5$
4	MSS	$P(M\|S, S, L_i)$,	$a = 25.0$

The parameters of functions (1), (3), and (4) were estimated from the data by maximum likelihood estimation. The parameters of function (2) are assumed to be reasonable. Hoopes and Greenough (1968) have presented a model for $P(M|S)$ and $P(M|M)$ that appears similar in form to the models presented here.

The tagging data listed also provided information on the conditional probability of molting given premolt length but unconditioned by molting history ($P(M|L_i)$). Figure 4 shows the unconditional probabilities estimated from the data and mathematically derived from the model of conditional probabilities.

Several models for the probabilities of molting for crabs less than 5 yr of age were constructed based upon Powell (1967). The molting probabilities for most populations are thought to lie between those presented in Tables 3 and 4. A growth function based upon Table 5 seems reasonable for the Kodiak population.

Growth Function

The models of length increment per molt and molting frequencies are combined to give the length-growth function. The model is sufficiently complicated that analytic expressions for the expectation and variance of "size at age" are intractable; hence, a computer simulation of the model was developed. Results of the simulation using the parameter estimates for the Kodiak population are given in Table 6.

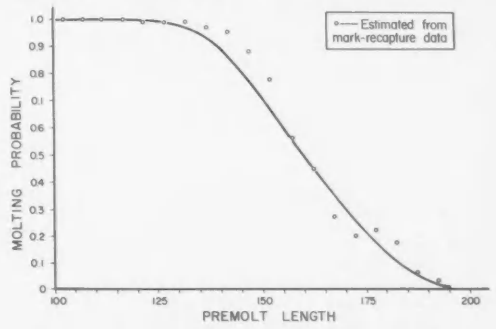

FIG. 4. The conditional probability of molting given only premolt length for male king crabs.

TABLE 3. Model for maximum molting probabilities.

	Number of molts per year							
Age	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	1.0
2	0	0	0	0	1.0	0	0	0
3	0	0	1.0	0	0	0	0	0
4	0	1.0	0	0	0	0	0	0
5	1.0	0	0	0	0	0	0	0
6	1.0	0	0	0	0	0	0	0

TABLE 4. Model for minimum molting probabilities.

	Number of molts per year							
Age	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	1.0	0
2	0	0	0	1.0	0	0	0	0
3	0	1.0	0	0	0	0	0	0
4	1.0	0	0	0	0	0	0	0
5	1.0	0	0	0	0	0	0	0
6	1.0	0	0	0	0	0	0	0

TABLE 5. Model of molting probabilities for the Kodiak population.

	Number of molts per year							
Age	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0.5	0.5
2	0	0	0	0.5	0.5	0	0	0
3	0	0.5	0.5	0	0	0	0	0
4	0.5	0.5	0	0	0	0	0	0
5	1.0	0	0	0	0	0	0	0
6	1.0	0	0	0	0	0	0	0

To test the sensitivity of the model to changes in parameters, the simulator for Kodiak males was run using the maximum and minimum molting frequencies for the first 4 yr (Tables 3 and 4) with all other parameters held constant. The differences in growth rate induced by changes in the early molting frequencies are great (Fig. 5); hence, the importance of obtaining molting frequency data on young crabs cannot be overemphasized. A translation of the logistic functions to increase the molting probabilities in older crabs for a given premolt length produces an increased growth rate as well but not as dramatic as changing the early molting frequencies.

TABLE 6. Growth simulation of individual king crab carapace length. $N = 2000$.

Age	Male king crabs			Female king crabs		
	Mean length	SD	Mean length ± 2 SD	Mean length	SD	Mean length ± 2 SD
1	12.58	1.71	9.16–16.00	12.65	1.72	9.21–16.09
2	33.44	5.97	21.49–45.39	33.40	5.90	21.60–45.20
3	57.85	12.08	82.00–33.69	57.35	12.00	45.35–69.35
4	78.87	16.90	45.08–112.67	77.36	14.84	48.80–105.92
5	95.52	18.86	57.80–133.24	91.01	14.31	62.39–119.63
6	113.62	20.24	73.15–154.09	103.67	12.74	78.19–129.15
7	131.57	19.38	92.82–170.33	114.63	10.92	92.79–136.47
8	146.97	16.40	114.17–179.76	123.88	9.25	105.38–142.38
9	158.29	12.60	133.13–183.45	131.57	8.13	115.31–147.83
10	165.89	9.70	146.48–185.28	137.59	7.30	122.99–152.19
11	170.90	8.36	154.19–187.61	143.64	6.61	130.42–156.86
12	174.63	7.47	159.70–189.56	148.49	6.20	136.09–160.89
13	177.59	6.74	164.10–191.07	152.69	6.00	140.69–164.69
14	179.66	6.36	166.95–192.38	156.42	5.96	144.50–168.34
15	181.63	5.96	169.71–193.55	159.73	5.91	147.91–171.55

TABLE 7. Simulated probabilities of possible ages of a king crab reaching various 10-mm length-classes.

Carapace length class midpoint	Age (years)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Males															
25		1.00													
50		.087	.762	.136	.015										
75			.198	.443	.286	.066	.007								
100			.001	.212	.341	.309	.119	.018							
125				.029	.123	.300	.336	.175	.034	.002					
150					.007	.050	.183	.294	.273	.142	.043	.008			
175						.001	.003	.020	.055	.108	.154	.179	.182	.163	.135
200										.016	.016	.062	.171	.297	.438
Females															
25		1.00													
50		.087	.762	.136	.015										
75			.251	.388	.292	.066	.004								
100			.001	.124	.318	.338	.177	.394	.002						
125					.009	.065	.216	.329	.269	.962	.015	.001			
150								.002	.014	.069	.164	.252	.243	.173	.083
175													.035	.198	.767

Size and Age Frequencies

The simulation of the model was used to obtain information on the relative frequencies of lengths a crab may reach at particular ages. The standard deviation of length at each age and the mean ±2 SD were estimated and are presented in Table 6. The frequency distribution of lengths for each age are unimodal and somewhat positively skewed. The simulation was also used to estimate the probability of a crab, having obtained a particular length, being a certain age. The results for selected 10-mm length-classes are presented in Table 7. The results of the simulation give information about the possibilities for growth in length of an individual crab. No inferences are to be made about age–length distributions for populations of crabs.

Discussion

The growth model of king crabs is not intended as an explanation of the underlying growth processes but is a synthesis of the empirical information into a growth model that mimics the possible growth in length of an individual crab.

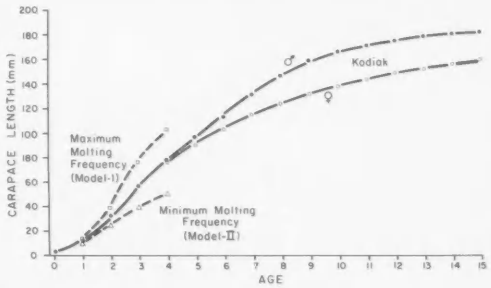

FIG. 5. Simulated mean carapace length as a function of age for Kodiak male king crabs and simulated mean carapace lengths under maximum and minimum probability of molting models for juvenile male king crabs.

Validation of this model is not possible at the present time and will not be possible until lengths of known age crabs become available. However, based on the available data a plausible growth model has been synthesized.

The model indicates that crabs that molt most frequently grow much faster until they reach a 115–125 mm in length. At this length their length increments begin to decline and their probability of molting becomes less. Slower growing crabs tend to catch up somewhat, since their molting probabilities and their length increments remain higher because of their smaller premolt lengths.

The major problem in building a model for crab growth is that the effect of age is confounded with premolt size. The ideal model would have length increments and molt probabilities as functions of age and premolt size. The age effect might explain why MMM crabs have larger length increments than MSS, MMS, and MSM crabs. If skip-molting is a function of age, and length increment decreases with age, then the MMM crabs may be younger than the other groups at similar premolt length and therefore exhibit larger length increments. The model presented here confounds the age effect with the premolt lengths. Until aging techniques are developed, little mechanistic refinement can be made upon this model.

The results of the simulation of individual growth indicate that large variability might exist in ages at particular sizes in king crab populations. The actual age distribution at various sizes would depend upon size- and age-specific natural mortality. Regardless of the specific form of the age variability for males of similar length, in a fixed-length-limit fishery, crabs of different ages are recruited into the exploitable population at the same time. The use of the classical stationary age-distribution population models should be used with caution.

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Swimming Stamina Differences Between Genotypically Distinct Forms of Rainbow (*Salmo gairdneri*) and Steelhead Trout

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TSUYUKI, H., AND S. N. WILLISCROFT. 1977. Swimming stamina differences between genotypically distinct forms of rainbow (*Salmo gairdneri*) and steelhead trout. J. Fish. Res. Board Can. 34: 996–1003.

Rainbow trout (*Salmo gairdneri*) homozygous for liver lactate dehydrogenase alleles *ldhH*α^A and *ldhH*α^B were artificially propagated and their swimming stamina compared. The time required to fatigue 50% of the Hα^AHα^A phenotypes in fixed water velocity tests was 2.3 times greater on the average than that of Hα^BHα^B phenotypes.

Likewise, LDH phenotypes Hα^AHα^A, Hα^AHα^B, and Hα^BHα^B of steelhead trout from the Thompson River were artifically propagated and their swimming stamina compared. In contrast to the rainbow trout, significant differences in stamina among the three phenotypes of steelhead were not evident in the stocks from this river nor between phenotypes Hα^AHα^B and Hα^BHα^B from another stream, the Vedder River, which has a very low frequency of the *ldhH*α^A allele. The stamina of young steelhead from the Thompson River was, however, 3.8 times greater than that of those from the Vedder River.

Key words: stamina, LDH, rainbow trout, steelhead, phenotype, swimming, fatigue

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On a fait reproduire artificiellement des truites arc-en-ciel (*Salmo gairdneri*) homozygotes pour les allélomorphes de la lactate déshydrogénase du foie *ldh H*α^A et *ldh H*α^B, et comparé leur vigueur de nage. Le temps requis pour fatiguer 50% des phénotypes Hα^AHα^A lors d'essais dans de l'eau de vitesse constante est en moyenne de 2.3 fois plus long que celui des phénotypes Hα^BHα^B.

De même, on a fait reproduire artificiellement les phénotypes de LDH Hα^AHα^A, Hα^AHα^B et Hα^BHα^B de truites steelhead du fleuve Thompson et comparé leur vigueur de nage. Contrairement à la truite arc-en-ciel, on n'a pu constater de différences significatives de vigueur entre les trois phénotypes de truites steelhead des stocks de ce fleuve, non plus qu'entre les phénotypes Hα^AHα^B et Hα^BHα^B d'un autre cours d'eau, la rivière Vedder, qui possède une très basse fréquence de l'allélomorphe de LDH Hα^A. La vigueur des jeunes truites steelhead du fleuve Thompson est cependant 3.8 fois plus grande que celle des individus de la rivière Vedder.

Received August 17, 1976
Accepted March 16, 1977

Reçu le 17 août 1976
Accepté le 16 mars 1977

THE swimming performance of salmonids has been investigated widely (Bainbridge 1960, 1962; Clancy 1963; Brett 1964, 1967; Webb 1971a, b; Brett and Glass 1973; Kutty and Saunders 1973). However, investigations on intraspecific differences in swimming performance of salmonids are relatively scarce.

Chinook salmon (*Oncorhynchus tshawytscha*), selected at the fry stage for high swimming stamina, returned in above average numbers to spawn as migratory adults (Burrows 1969). Bams (1967) found that sockeye salmon (*O. nerka*) fry propagated under different conditions showed differences in swimming stamina, which may be defined as the time taken to fatigue during a swimming test at a reasonably high water velocity. Differences in swimming stamina were noted between early and late runs of adult coho salmon (*O. kisutch*) (Paulik and Delacy 1957). However, this difference may simply reflect differences in the state of maturity.

The finding (Northcote et al. 1970; Huzyk and Tsuyuki 1974) of allelic differences in the lactate dehydrogenases (LDH) (L-lactate: NAD oxidoreductase, EC 1.1.1.27) in rainbow and steelhead trout (both *Salmo gairdneri*) provided the opportunity to compare swimming stamina in rainbow

Printed in Canada (J4513)
Imprimé au Canada (J4513)

trout phenotypes $H\alpha^AH\alpha^A$ and $H\alpha^BH\alpha^B$. The relative swimming stamina of young Thompson River steelhead trout phenotypes $H\alpha^AH\alpha^A$, $H\alpha^AH\alpha^B$, and $H\alpha^BH\alpha^B$ was determined. The Thompson River fish were also compared with steelhead phenotypes $H\alpha^BH\alpha^B$ and $H\alpha^AH\alpha^B$ from the Vedder River.

Materials and Methods

Rainbow Trout

Experimental fish — Adult rainbow trout were obtained in the late spring of 1971 from the inlet stream to Loon Lake, just north of Cache Creek, British Columbia. The LDH phenotype was determined by electrophoresis of a small sample of blood plasma and each fish was finclipped for future identification. The appropriate fish were artificially crossed to produce offspring homozygous to $ldhH\alpha^A$ and $ldhH\alpha^B$ by a method to be described later. Offspring from these crosses were held indoors at the Vancouver Laboratory in separate 910-ℓ oval tanks with minimum water flow. The water supply consisted of dechlorinated city water at ambient temperatures administered via surface spray nozzles to each tank. Initially the fish were fed Oregon Moist Pellets, followed by a meat diet. When the fish reached a fork length of 5–6 cm, swimming stamina tests were conducted.

The trout were prepared for testing by placing appropriate numbers of each phenotype into separate but identical 230-ℓ oval tanks 2 wk before each stamina test. The water supply was unchanged in quality and temperature from that used previously. It was delivered by underwater nozzles adjusted to produce a mean flow of approximately 2.5 body lengths (BL)/s. The fish were observed to occupy the outer areas of the tanks where the flow was greatest. The meat diet was terminated 24 h before each test.

Size variance of each stock population was not accurately determined before any test. Fish to be preconditioned and later tested were selected for approximate uniformity in size within and between phenotypes. The fork length of each experimental fish was determined after each stamina test. No fish was tested more than once.

Rainbow trout tests — A swim tunnel belonging to the British Columbia Research Council (Howard 1973) was used. Briefly, this apparatus consisted of three parallel clear plexiglass tubes, each 9 cm in diameter and 95 cm in length. Dechlorinated city water at the acclimation temperature was recycled through the tubes from a 300-ℓ reservoir at variable flow rates, measured according to the time required to deliver a known volume of water through the tunnel. To encourage swimming, an electric field of approximately 6 *V* DC was set up between ring electrodes installed near a removable screen barrier located at the downstream end of each tube. Temperatures were controlled to within ±0.5°C. The LDH phenotypes occupied separate tubes during any one test. Howard (unpublished data) demonstrated that in coho salmon "no significant difference occurred in the ability of three comparable groups of fish to swim in the three tubes against identical current velocities." To avoid possible tunnel bias, however, the tube occupied by a single phenotype was not the same in all tests.

Swim test procedure — Swimming performance of fish has been investigated in various ways by different investigators. Some have measured "burst speed" at low water velocity (Bainbridge 1960, 1962; Wardle 1975). Others have determined the water velocity at which fatigue occurs, using continual incremental increases in water speed (Brett 1964, 1965, 1967; Bams 1967; Stevens and Randall 1967a, b; Burrows 1969; Webb 1971a; Griffiths and Alderdice 1972; Howard 1975). Still others have determined the time required to fatigue at a fixed water velocity (Paulik and Delacy 1957; Clancy 1963; Brett 1964, 1967; Kutty and Saunders 1973). Brett (1964) reported that the fixed-velocity method "provides a useful basis for comparative studies of performance under different environmental conditions and allows the use of data where not all the fish fatigue by the end of the test time." In this study comparing the swimming stamina of trout of different LDH phenotypes, the fixed water velocity method was used. In any one experiment, the two phenotypes were compared under as identical experimental conditions as possible. Between experiments the conditions were varied somewhat to accommodate the needs of the growing test fish. Therefore, the relative performances of the two phenotypes within any single test, with its own particular set of conditions, was considered meaningful. No specific attempt was made to duplicate a previous test condition.

The rainbow trout phenotypes were transferred from their "preconditioning" tanks and placed in the swim tunnel on the morning of the test. The downstream electric field was switched on, and the fish were allowed to become familiar with the tunnel environment for 1 h at a water velocity of 2.5 BL/s. Preliminary runs with fish of the same approximate size were used to determine the appropriate final test water velocity. After 1 h, the water velocity was increased over a 1.0-min interval to one half the final predetermined water velocity. The fish remained at this velocity for 20 min; the final test water velocity was then achieved over another 1.0-min interval. The time when the final velocity was reached was designated t_0 for each experiment. The test water velocity, V_t, remained at this level until the end of the test. As each fish fatigued, as indicated by its inability to remove itself from the screen, it was withdrawn from the tunnel, the time recorded, and the fork length measured. The experiment continued until at least 50% of both populations had fatigued. Those remaining were removed and measured. The small number of trout that would or could not swim before the start of the experiment at V_t were eliminated from the test and not included in the analysis.

STEELHEAD TROUT

Experimental fish — Mature migrating steelhead trout were captured from the Thompson River during the fall of 1973. The methods used to capture, handle, transport, and maintain the fish as well as the techniques used in selective artificial breeding are to be described elsewhere. After attaining a fork length of 5–6 cm, the offspring from these crosses were used for swimming stamina studies.

Young Vedder River steelhead trout were obtained from the Abbotsford Hatchery, B.C. Department of Recreation and Conservation. The fish were offspring from wild stocks of Vedder River steelhead captured and artificially spawned in the spring of 1974, the same year as the Thompson River steelhead. Both steelhead stocks were maintained in dechlorinated city water and fed Oregon Moist Pellets. All fish were acclimated to the test temperature for a period of at least 2 wk and starved for 24 h before testing. They were simultaneously trained in separate 230-ℓ oval tanks at 2.5 BL/s.

The steelhead were selected for uniformity of length before testing in the tunnel. As with the rainbow trout, no fish was tested more than once.

Steelhead trout tests — A 28-cm diameter swim tunnel belonging to the International Pacific Salmon Fisheries Commission was used. A large volume of water, 6400 ℓ, was recycled through the tunnel at controlled velocities. The length of the single tunnel was 270 cm. A downstream screened butterfly valve was constructed and used to capture exhausted fish. To become impinged on the screen, the fish had to pass through a 6 V DC electric field formed by three ring electrodes placed 80 on upstream of the screen. The water used for the tests was the same dechlorinated city water. The temperature in the system generally was maintained at $\pm 0.5°$ C for the duration of any test. Additional cooling was found necessary during the warm summer months, as the tunnel, owing to its size, was operated outside the laboratory. Water velocity in the tunnel was calibrated by relating pump revolutions with the readings from a Gurley flow meter. A more thorough description of the apparatus may be obtained from the International Pacific Salmon Fisheries Commission, New Westminster, B.C.

Swim test procedure — Steelhead trout were placed in the large tunnel approximately 16 h before the start of the test at the water velocity and temperature of the acclimation period. The electric field was not switched on until the start of each test.

At the start of a test, the water velocity was elevated to test velocity V_t over a 40-min time period. The technique varied from that used in the rainbow trout tests in that incremental increases in water velocity occurred every 5 min. Preliminary tests defined the appropriate test velocities. The differences between these and the acclimation velocity were divided equally over 5-min intervals to achieve V_t after approximately 40 min. All the steelhead occupied the single tunnel simultaneously. The LDH phenotype of each fish was determined after the experiments by electrophoretic analyses of liver homogenates. The size of the tunnel facilitated the simultaneous testing of large numbers of steelhead trout of different phenotypes and stocks. Thus, all fish within each experiment were subjected to identical test conditions.

SWIM FATIGUE TIME

The method used for estimating swimming stamina is basically that used for sockeye salmon (Brett 1964) where the fatigue times of the individuals of a group are determined at a constant water velocity. Logarithms of the fatigue times of individual fish are plotted against the probit of the cumulative percentage fatigued. Calculated probit regression lines were then fitted to the fatigue times. These lines provided the provisional means and standard deviations used in the calculations of improved estimates. The methods used for the computation of final solutions to the truncated distributions are described by Bliss (1937). The time required to fatigue 50% of the fish tested (FT50), graphically expressed as a probit of 5.0, is used as an index of swimming stamina for the group (Brett 1964). The Student's *t*-test was used to determine the statistical significances of FT50 value differences based on the transformed data. (Snedecor and Cochran 1967).

Results

COMPARATIVE SWIMMING STAMINA

Loon Lake rainbow trout phenotypes $H\alpha^AH\alpha^A$ *and* $H\alpha^BH\alpha^B$ — The responses of rainbow trout phenotypes $H\alpha^A$ $H\alpha^A$ and $H\alpha^BH\alpha^B$ to stamina tests are illustrated in Table 1. The three tests were carried out under a range of experimental conditions. The FT50 of the $H\alpha^AH\alpha^A$ phenotype ranged from 1.6 (test 2) to 3.2 (test 3) times greater than that of the $H\alpha^BH\alpha^B$, an average of 2.3 times. This does not include an extension of test 1 in which fish not fatigued were held overnight in the tunnel at a water velocity of 16.16 cm/s and tested again the following day at a higher water speed of 27.70 cm/s. In this case the FT50 of phenotype $H\alpha^AH\alpha^A$ was 6.18 times greater than that of $H\alpha^BH\alpha^B$. In two out of three tests in Table 1, the $H\alpha^AH\alpha^A$ phenotypes possessed significantly greater swimming stamina than the $H\alpha^BH\alpha^B$.

Two additional stamina tests not shown in Table 1 were conducted on the Loon Lake trout. On September 21, 1973 these fish were approximately 26–27 mo old. We noted at the time that the $H\alpha^AH\alpha^A$ phenotypes held at Cultus Lake for acclimation, as well as the stock at the Vancouver Laboratory, were becoming slightly darker in color, indicating perhaps the onset of secondary characteristics of sexual maturity. In contrast, the $H\alpha^BH\alpha^B$ phenotypes remained silver

TABLE 1. Comparative swimming stamina of Loon Lake rainbow (*Salmo gairdneri*) trout LDH phenotypes $H\alpha^AH\alpha^A$ and $H\alpha^BH\alpha^B$.

	Test		
	1 (Jan. 13, 1972)	2 (Mar. 16, 1972)	3 (Mar. 17, 1972)
Mean fork length			
$H\alpha^AH\alpha^A$(cm) ± SE (*N*)	4.58 ± 0.262(20)	4.75 ± 0.312(16)	4.97 ± 0.343(16)
$H\alpha^BH\alpha^B$(cm) ± SE (*N*)	4.57 ± 0.272(20)	4.83 ± 0.325(16)	5.01 ± 0.347(16)
Temp (°C)	11.0 ± 0.5	13.6 ± 0.5	13.0 ± 0.5
V_f(cm/s)	16.16	29.00	30.00
Duration of test (min)	485	555	270
Fatigued (%)			
$H\alpha^AH\alpha^A$	55	25	56
$H\alpha^BH\alpha^B$	75	63	100
FT50 (min) ± SE			
$H\alpha^AH\alpha^A$	326 ± 73	640 ± 148	214 ± 64
$H\alpha^BH\alpha^B$	162 ± 41	390 ± 80	77 ± 21
$*P\frac{H\alpha^AH\alpha^A}{H\alpha^BH\alpha^B}$	0.030	0.090	0.005

*Student's *t*-test, probability of no difference in mean fatigue time, FT50; two-tailed.

in color. The dark color of the $H\alpha^AH\alpha^A$ phenotypes became progressively more pronounced to the extent that the two phenotypes could be readily distinguished. A swim test conducted on October 18, 1973 showed a marked decrease in the relative stamina of the $H\alpha^AH\alpha^A$ compared with the $H\alpha^BH\alpha^B$ phenotypes. An additional test on December 20, 1973 showed a more drastic reduction in the swimming stamina of the $H\alpha^AH\alpha^A$ phenotypes. The FT50 values of the $H\alpha^AH\alpha^A$ phenotype in the October and December tests were respectively only 0.79 and 0.28 that of the $H\alpha^BH\alpha^B$ phenotype. During these later tests, the $H\alpha^BH\alpha^B$ phenotypes performed as before. On the other hand, the $H\alpha^AH\alpha^A$ phenotypes behaved erratically, although no outward signs of fatigue were indicated. The latter fish generally failed to hold the usual position in the tunnel and there was a marked tendency for them to swim downstream to the rear barrier. It would be of interest to determine whether actual differences in the timing of sexual maturation between the two phenotypes exist as was suggested by differences in coloration.

Thompson River phenotypes $H\alpha^AH\alpha^A$, $H\alpha^AH\alpha^B$, *and* $H\alpha^BH\alpha^B$ — For testing steelhead, the larger swim tunnel was used; the fish were larger, and in the numbers needed for the test they tended to be crowded in the smaller tunnel used for testing the Loon Lake rainbow trout. Approximately 200 fish were placed in the large tunnel at one time, making possible the simultaneous testing of all three phenotypes. Variations in the conditions for any one test comparing the different phenotypes were therefore minimized. In each succeeding test the average size of the fish selected tended to be larger and in the absence of adequate temperature control for the large volume of water in the tunnel, the experiments were conducted at the water temperature found for that day. It was possible, however, to maintain a relatively uniform water temperature for the duration of the test. Although the water temperatures differed in the two tests and the FT50 values were higher at the warmer temperature, the swimming stamina between phenotypes $H\alpha^AH\alpha^A$ and $H\alpha^BH\alpha^B$ in each test (Table 2) were very nearly the same in contrast to the large differences observed between the Loon Lake rainbow trout phenotypes.

Thompson and Vedder steelhead phenotypes — Thompson River steelhead, composed of a 50:50 mixture of $H\alpha^AH\alpha^A$ and $H\alpha^AH\alpha^B$ fish, were tested simultaneously in the 28-cm tunnel against a 40:60 mixture of $H\alpha^AH\alpha^B$ and $H\alpha^BH\alpha^B$ Vedder River steelhead. The results (tests 6 and 7) are shown in Table 3. All Vedder fish that were reared outdoors in large circular tanks were still distinguishable by their coloration from the Thompson fish reared indoors at the time the experiments were carried out. However, as an added precaution, the Thompson steelhead stock used for the test was devoid of phenotype $H\alpha^BH\alpha^B$ to avoid any possible confusion with Vedder fish of the same phenotype. Phenotypes $H\alpha^AH\alpha^B$, common to both rivers, were identified by color difference. It is noted that the Vedder steelhead used in this study has an unusually high frequency of phenotype $H\alpha^AH\alpha^B$ compared

TABLE 2. Comparative swimming stamina of Thompson River steelhead trout LDH phenotypes $H\alpha^AH\alpha^A$, $H\alpha^AH\alpha^B$, and $H\alpha^BH\alpha^B$.

	Test	
	4 (May 14, 1975)	5 (June 4, 1975)
Mean fork length		
$H\alpha^AH\alpha^A$ (cm) ± SE (*N*)	9.35 ± 0.253(40)	10.66 ± 0.377(33)
$H\alpha^AH\alpha^B$ (cm) ± SE (*N*)	9.57 ± 0.109(101)	10.93 ± 0.145(82)
$H\alpha^BH\alpha^B$ (cm) ± SE (*N*)	9.43 ± 0.172(58)	10.65 ± 0.334(36)
Temp (°C)	11.0 ± 0.5	9.2 ± 0.2
V_f (cm/s)	50.30	49.80
Duration of test (min)	625	354
Fatigued (%)		
$H\alpha^AH\alpha^A$	65	73
$H\alpha^AH\alpha^B$	67	74
$H\alpha^BH\alpha^B$	67	69
FT50 (min) ± SE		
$H\alpha^AH\alpha^A$	190 ± 103	120 ± 34
$H\alpha^AH\alpha^B$	230 ± 83	105 ± 40
$H\alpha^BH\alpha^B$	185 ± 101	122 ± 40
$P\frac{H\alpha^AH\alpha^A}{H\alpha^AH\alpha^B}$	>0.5	>0.5
$P\frac{H\alpha^AH\alpha^A}{H\alpha^BH\alpha^B}$	>0.5	>0.5
$P\frac{H\alpha^AH\alpha^B}{H\alpha^BH\alpha^B}$	>0.5	>0.5

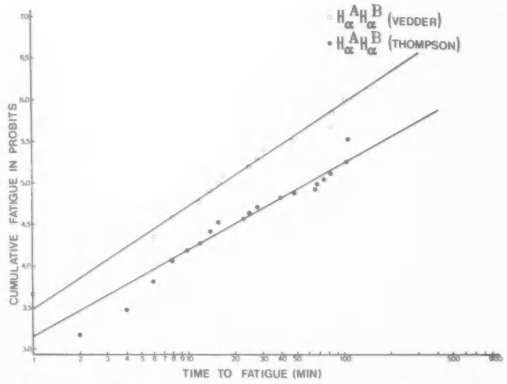

FIG. 1. Calculated regression lines (Bliss 1937) relating log time to fatigue to probit of cumulative proportion fatigued in Thompson River and Vedder River $H\alpha^AH\alpha^B$ phenotypes, illustrating graphic evaluation of the FT50 values (probit 5.00).

to adults from the same river surveyed earlier (Huzyk and Tsuyuki 1974).

Again, unlike the Loon Lake rainbow trout, no significant differences in swimming stamina were observed between the two phenotypes of steelhead from the Vedder river ($P > 0.50$). However, the average FT50 values of the Thompson River phenotypes $H\alpha^AH\alpha^A$ and $H\alpha^A\alpha^B$ were about 3.8 times greater than phenotypes $H\alpha^AH\alpha^B$ and $H\alpha^BH\alpha^B$ from the Vedder River, a statistically significant difference. This order of difference is similar to that found between phenotype $H\alpha^AH\alpha^A$ and $H\alpha^BH\alpha^B$ of rainbow trout from Loon Lake. Unfortunately phenotype $H\alpha^AH\alpha^A$ from the Vedder River was not available for direct comparison. Figure 1 illustrates graphically part of the results of test 6 comparing the swimming stamina of the Thompson River $H\alpha^AH\alpha^B$ phenotype to the Vedder River $H\alpha^AH\alpha^B$ phenotype.

Discussion

Each LDH phenotype of rainbow and steelhead trout exhibited a wide variation in measured swimming stamina. The rainbow trout $H\alpha^AH\alpha^A$ phenotypes, however, are considered superior to the $H\alpha^BH\alpha^B$ phenotypes by virtue of the higher proportion of longer fatigue times in the former group.

Within each of the Thompson and Vedder steelhead stocks tested there was an unexpected absence of phenotypic differences in mean swimming stamina. However, the proportion of superior swimmers differed significantly in the

TABLE 3. Comparative swimming stamina of Thompson River (T) steelhead trout LDH phenotypes $H\alpha^AH\alpha^A$, $H\alpha^AH\alpha^B$ and Vedder River (V) steelhead trout LDH phenotypes $H\alpha^AH\alpha^B$, $H\alpha^BH\alpha^B$.

	Test	
	6 (June 17, 1975)	7 (June 25, 1975)
Mean fork length		
$H\alpha^AH\alpha^A$ (T) (cm) ± SE (*N*)	9.94 ± 0.288(36)	9.84 ± 0.176(58)
$H\alpha^AH\alpha^B$ (T) (cm) ± SE (*N*)	10.14 ± 0.225(46)	9.77 ± 0.246(41)
$H\alpha^BH\alpha^B$ (V) (cm) ± SE (*N*)	10.10 ± 0.371(27)	9.60 ± 0.297(38)
$H\alpha^AH\alpha^B$ (V) (cm) ± SE (*N*)	9.78 ± 0.348(31)	9.35 ± 0.536(19)
Temp (°C)	10.0 ± 0.1	9.7 ± 0.2
V_f (cm/s)	49.30	49.80
Duration of test (min)	357	142
Fatigued (%)		
$H\alpha^AH\alpha^A$ (T)	53	64
$H\alpha^AH\alpha^B$ (T)	63	61
$H\alpha^BH\alpha^B$ (V)	81	89
$H\alpha^AH\alpha^B$ (V)	85	84
FT50 (min) ± SE		
$H\alpha^AH\alpha^A$ (T)	67 ± 50	60 ± 22
$H\alpha^AH\alpha^B$ (T)	59 ± 24	99 ± 75
$H\alpha^BH\alpha^B$ (V)	26 ± 11	16 ± 3
$H\alpha^AH\alpha^B$ (V)	17 ± 7	18 ± 6
$P\frac{H\alpha^AH\alpha^A\ (T)}{H\alpha^BH\alpha^B\ (V)}$	0.045	0.001
$P\frac{H\alpha^AH\alpha^B\ (T)}{H\alpha^AH\alpha^B\ (V)}$	0.001	0.010
$P\frac{H\alpha^AH\alpha^A + H\alpha^AH\alpha^B\ (T)}{H\alpha^AH\alpha^B + H\alpha^BH\alpha^B\ (V)}$	0.025	0.001

two streams. The Thompson fish possessed far greater swimming stamina. A further difference between the stocks in the two rivers was noted. In the Thompson River fish, all three phenotypes are present in the wild, while only the $H\alpha^BH\alpha^B$ and $H\alpha^AH\alpha^B$ phenotypes have been found in the Vedder River stock. The $H\alpha^A$ allele is scarce in steelhead from the Vedder River or other coastal (lower mainland and Vancouver Island) streams examined. The similarity in the swimming stamina for all three phenotypes from the Thompson River could suggest that phenotypic differences have been eliminated or at least minimized as a result of the possible existence at one time on this system of water flow or other conditions not favorable to fish with low stamina. The $H\alpha^AH\alpha^A$ phenotypes occur in high frequencies in rainbow trout from the upper watersheds of the Columbia and Thompson rivers and in steelhead trout from the Thompson and Chilcotin rivers (Huzyk and Tsuyuki 1974). The latter rivers are tributaries to the Fraser River but are located well above the fast waters in the Fraser River canyon, suggesting an association of the $H\alpha^AH\alpha^A$ variant with higher water velocity. Somewhat similar geographic separation of steelhead trout with low and high frequencies of the $H\alpha^A$ allele has been reported by Allendorf (1975). The $H\alpha^A$ allele, reported previously (Williscroft and Tsuyuki 1970; Utter and Hodgins 1972; Huzyk and Tsuyuki 1974), occurred in high frequency in the Columbia River system above the crest of the Cascade Mountain range. From his extensive studies, Allendorf (1975) suggested the existence of two taxonomic groups of steelhead, the coastal group characterized by a low frequency and the inland group by a high frequency of the *ldh*$H\alpha^A$.

The blood lactate level in the rainbow trout is known to increase throughout the entire period of vigorous muscular exertion (Black 1958; Black et al. 1959; 1966). More recently it has been reported that blood lactate levels do not show a net increase at $< 93\%$ of critical swimming velocity for the individual (Driedzic and Kiceniuk 1976). Rapid increases occurred at higher water velocities or following cessation of muscular activity. Gluconeogenic activity, particularly in the gills (Bilinski and Jonas 1972) has been suggested (Driedzic and Kiceniuk 1976) as a possible mechanism for eliminating blood

lactate. An increase in hydrogen ion concentration has been reported (Black et al. 1959) to occur during the first 6 min of vigorous exercise and this change was associated with a significant reduction in maximum swimming speed of yearling trout (Black 1955). Impairment in the oxygen combining capacity of blood has been noted in marine fish (von Buddenbrock 1938) and in carp (Secondat and Diaz 1942) following severe exercise. The Bohr effect, or the effect of acid in reducing the affinity of hemoglobin for oxygen, is most pronounced in one of the two classes of hemoglobin in salmon. The more electronegative molecular species in rainbow trout (Ronald and Tsuyuki 1971), which comprises some 60% of the total hemoglobin (Hashimoto and Matsuura 1959), is affected profoundly by small decreases in pH (Tsuyuki unpublished data), much like the "fast" hemoglobin of Pacific salmon (Hashimoto et al. 1960). A rapid increase in blood lactate, therefore, may severely reduce the oxygen supply to the tissues. Liver tissue is known to metabolize lactate at a rapid rate (Bilinski and Jonas 1972). It is in this tissue and in the red blood cells (Bailey et al. 1976) that the $H\alpha^A$ allele is most strongly expressed. Structural differences in the lactate dehydrogenases between phenotypes $H\alpha^A H\alpha^A$ and $H\alpha^B H\alpha^B$ could well influence the rate of dissipation of lactate and hence contribute to postponing the onset of fatigue in the former.

Although LDH is intimately associated with the catabolism of the accumulated lactate following vigorous muscular exertion, we realize that differences in the allelic forms of this enzyme is only one of many factors that may influence swimming performance. The absence of major differences in the stamina of Thompson River steelhead phenotypes suggests that differences in LDH may be masked by other factors. For example, simultaneous testing in one tunnel of low and high stamina fish from the same stream may influence their performance relative to each other. However, the consistently low stamina of the Vedder relative to the Thompson steelhead when tested simultaneously argues against such influence. Due to the rarity of the $ldhH\alpha^A$ gene from the steelhead from the Vedder River, we were unable to test the stamina of fish homozygous to this gene against the obviously low stamina $H\alpha^B H\alpha^B$ phenotype. The results from Loon Lake rainbow trout suggest that phenotypic differences in stamina are maximized in stocks not already in some way selected for high performance.

Artificial propagation programs for resident rainbow trout should take into account the superior swimming stamina of phenotype $H\alpha^A H\alpha^A$. A direct correlation between swimming stamina and vulnerability to predation has been indicated for sockeye salmon fry (Bams 1967). Steelhead from the Thompson River, characterized by their superior swimming ability, and perhaps those from the Chilcotin River, have a high frequency of the $H\alpha^A$ allele. These sources should be considered seriously as parental stocks in future artificial propagation programs in British Columbia. Genetic differences between stocks or populations, exemplified in the current study, may be more prevalent than current knowledge would suggest. Further exploration to determine genetically induced differences between stocks would seem advisable prior to the introduction of large-scale genetic mixing in transplanting and restocking programs.

Acknowledgements

We are grateful to Dr T. Howard and Mr J. Monroe, B.C. Research Council, who provided swim testing facilities. We also thank Mr I. Williams and others of the International Pacific Salmon Fisheries Commission for the use of their swim tunnel and holding facilities. The Abbotsford Hatchery, B.C. Department of Recreation and Conservation, Fish and Wildlife Branch, kindly provided young Vedder River steelhead trout. We extend special thanks to Dr D. F. Alderdice, Pacific Biological Station, for his constructive criticism and assistance in the preparation of this manuscript. Dr P. A. Larkin, University of British Columbia, kindly provided valuable assistance in the statistical analyses of the data.

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Plankton Dynamics and Nutrient Enrichment of the Scotian Shelf

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FOURNIER, R. O., J. MARRA, R. BOHRER, AND M. VAN DET. 1977. Plankton dynamics and nutrient enrichment of the Scotian Shelf. J. Fish. Res. Board Can. 34: 1004–1018.

Four seasonal cruises were conducted on a 270-km-long transect normal to the coast of Nova Scotia. Most biological variables measured along this transect show maximum values in the outer 90 km. These maxima usually occur closely associated with an oceanic front which is a consistent feature of this region. Enhanced vertical transport of nutrients is postulated to occur along this front, although the mechanism is unknown. A model proposed several years ago to explain shelf enrichment off the northeastern United States was examined and found to be consistent with the Scotian Shelf data. Sporadic advection of nutrient-rich Slope Water onto the shelf at the average rate of 0.33 $cm \cdot s^{-1}$ would, upon entering the euphotic zone, satisfy 20% of phytoplankton nutrient requirements during the spring and summer. Recycling would account for the remaining 80%.

Key words: phytoplankton, zooplankton, enrichment, Scotian Shelf, excretion, fronts, nutrients, productivity, advection, recycling

FOURNIER, R. O., J. MARRA, R. BOHRER, AND M. VAN DET. 1977. Plankton dynamics and nutrient enrichment of the Scotian Shelf. J. Fish. Res. Board Can. 34: 1004–1018.

Quatre croisières saisonnières ont été effectuées sur une ligne de 270 km de longueur perpendiculaire à la côte de la Nouvelle-Ecosse. La plupart des variables biologiques mesurées le long de cette section montrent des valeurs maximales dans les 90 km du large. Ces maximums se rencontrent ordinairement en étroite association avec un front océanique qui est une caractéristique uniforme de cette région. On suppose qu'il se produit le long de ce front un transport vertical accentué d'éléments nutritifs, quoique le mécanisme n'en soit pas connu. Nous examinons le modèle proposé il y a plusieurs années pour expliquer l'enrichissement du plateau du large du nord-est des Etats-Unis et le trouvons conforme aux données du plateau néo-écossais. Une advection sporadique de l'eau de pente riche en éléments nutritifs sur le plateau à la vitesse moyenne de 0.33 $cm \cdot s^{-1}$ suffirait, en pénétrant dans la zone euphotique, à satisfaire à 20% des besoins du phytoplancton en éléments nutritifs durant les mois de printemps et d'été. Le recyclage pourrait expliquer la balance de 80%.

Received October 28, 1976
Accepted March 15, 1977

Reçu le 28 octobre 1976
Accepté le 15 mars 1977

THE waters overlying the world's continental shelves are among the most productive oceanic regions (Hennemuth 1975). Koblentz-Mishke et al. (1970) place the average level of net primary production in these areas at 200 g $C/(m^2 \cdot yr)$. This is about midway between the high primary production values observed in some coastal upwelling areas (>350 g $C/(m^2 \cdot yr)$, and those of a poor region such as the Sargasso Sea where the annual productivity averages <100 g $C/(m^2 \cdot yr)$. Sufficient data to estimate the annual productivity for the ocean waters off Canada's eastern coast are not available. However, the high fertility of this region may be inferred from the large commercial fish stocks which attract fishermen from all the major European fishing nations (Grant and Rygh 1973).

Printed in Canada (J4627)
Imprimé au Canada (J4627)

For the Scotian Shelf, the continental shelf adjacent to Nova Scotia, evidence of high productivity is likewise indirect and somewhat subjective. The underlying mechanisms responsible for fertility of the shelf as a whole have not been subject to intensive investigation. There are local areas on the shelf that appear to be decidedly richer than the average level of productivity based on fishery yields, implying some special or extraordinary physical mechanisms. For example, the area surrounding the southwestern tip of Nova Scotia supports intense fisheries for lobster and herring (Kohler 1968) and in addition possesses the largest population of nonbreeding surface feeding birds in the northwest Atlantic (R. Brown, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication). Lauzier (1967), using seabed drifter returns, suggested that localized upwelling was occurring in this area. More recently Garrett and Loucks (1976)

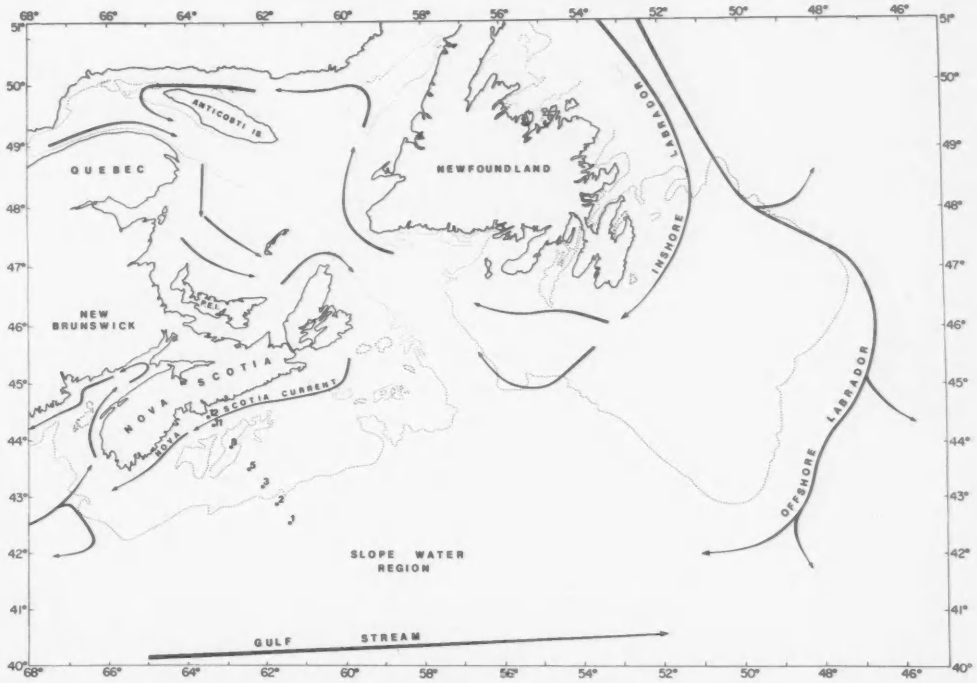

FIG. 1. The Scotian Shelf delimited by the 200 m contour, the major stations described in the text, and a summary of the surface circulation in this area based on Sutcliffe et al. (1976a).

have hypothesized that centrifugal upwelling may be the operative mechanism.

A second area reputed to possess higher than average productivity is a narrow band along the shelf break (Schroeder 1955; Grant and Rygh 1973; Brown et al. 1975). The evidence is mostly circumstantial, although Schroeder reported finding more fish (both in weight as well as numbers) off the southern tip of the Scotian Shelf than any place else south to Chesapeake Bay. Evidence from work done off the east coast of the United States suggests that enhanced productivity at the shelf break may be a general phenomenon. Observations on zooplankton abundance (Clarke 1940, Grice and Hart 1962), benthos (Sanders et al. 1965), and fish stocks (Schroeder 1955) show higher levels of standing stocks than on either side of the shelf break–slope region. Despite these indications to the contrary a widely held belief (see Smayda 1975 for review) is that productivity decreases with increasing distance from shore.

The purpose of this report is to describe the initial results of a program to investigate the level of biological activity across the Scotian Shelf and into Slope Water with a special emphasis on nutrient gradients, recycling, and possible sources of supply.

Materials and Methods

Four cruises are considered here, one in each of the four seasons: May 28 to June 3, 1974; November 4–8, 1974, March 3–6, 1975, and August 25–29, 1975. Each cruise had the same format with a single transect of 12 stations run normal to the coast from Halifax to a point about 60 km beyond the shelf break. At each of the seven stations, numerically identified in Fig. 1, a basic series of observations was made that included hydrography, nutrient chemistry, and plankton biomass. In addition, usually three and sometimes four of these stations (1, 3, 8, and 11) were occupied for 18 h to make diurnal observations at 6-h intervals. At these longer stations experimental observations were made of primary productivity and zooplankton excretion rates. The remaining five stations, not numerically identified, were solely hydrographic.

This transect was chosen because it intersects every water type present on the shelf, providing a variety of shelf characteristics over a short distance. A second reason for selecting this line is that hydrographic observations have been made there continuously since 1950 (Taylor 1961, 1966; de la Ronde 1972); thus the distribution of physical variables for the area is

reasonably well known. The depth of water over the shelf varies between 100 and 150 m, except for Emerald Basin, (Station 8), located about midway across the shelf, which approaches 300 m.

Vertical profiles of temperature and salinity were taken with a Guildline CTD. Back up observations of temperature and salinity were made using a bathythermograph and salinities from water samples at discrete depths. Subsurface light intensities were measured with a Lambda model LI-192S underwater quantum sensor (Lambda Instrument Corp., Lincoln, Nebr.).

For the diurnal stations, samples were taken with 5- or 12-ℓ Niskin bottles from six depths in the euphotic zone (100, 50, 20, 10, 3, and 1% of surface light intensity) and at standard depths below the euphotic zone. At all other stations standard depths were used. Samples for productivity measurement and ATP analysis were filtered through 153-μm mesh before use. Nutrient samples (except silicate) were filtered through Gelman GFA filters before storage in Whirlpak® plastic bags and plastic bottles (phosphate, nitrate, nitrite, and silicate) or in acid-washed glass bottles (ammonia and urea) and frozen at −20 to −30°C until analyzed. (Plastic bags were used only on the November cruise.) Chlorophyll was measured continuously over the entire transect using a Turner Designs model 10 continuous-flow fluorometer which monitored ship flow-through with an inlet about 1 m below the surface. This instrument was calibrated several times each day. ATP was determined by the method of Holm-Hansen and Booth (1966) with modifications (Sutcliffe et al. 1976b), using the ATP photometer model 2000 manufactured by JRB, Inc., La Jolla, Calif. Chlorophyll *a* was estimated spectrophotometrically using the SCOR-UNESCO trichromatic equations. All chemical analyses are according to Strickland and Parsons (1972).

Rates of carbon assimilation were estimated from the ^{14}C method of Steeman-Nielsen (1952) on samples from the six depths in the euphotic zone at the diurnal stations. Incubations were performed using an on-deck incuabtor with light attenuators and cooled by surface water. Incubation times ranged from the length of the daylight period to 24 h. After incubation, the samples were filtered onto Millipore® HA filters; the filters were rinsed with filtered seawater and then placed in scintillation vials containing a water compatible cocktail (2:1 vol/vol, 6 g PPO + 75 mg POPOP/ℓ and Triton X-100). The vials were kept refrigerated until counted in a Packard Tricarb scintillation counter immediately following each cruise. Counting efficiencies were determined using automatic external standardization.

Samples for protozoan biomass determination were unconcentrated and preserved with basic Lugol's solution. Volume was estimated microscopically assuming a specific gravity of 1.0 and then a volume to dry weight conversion was made by multiplying by 0.13 (Eppley et al. 1973). To estimate zooplankton biomass, oblique tows were taken through the water column with a 239-μm mesh, 0.75-m net. Dry weights were determined by filtering the zooplankton onto preweighed glass fiber filters, rinsing with distilled water, and drying at 60°C until constant weight was achieved.

To measure zooplankton respiration and excretion, net tows were taken through the euphotic zone at 6-h intervals over an 18-h period. Six experimental bottles of 1-ℓ capacity were prepared with a zooplankton concentration of approximately 100 mg dry wt/ℓ after removal of all soft-bodied forms likely to have been damaged in capture (always, in our case, a small fraction of the total biomass). An analysis of the results showed no crowding effects around this concentration. Using siphons, the water in the bottles was replaced twice with surface water, and the bottles were incubated for 4 h at the surface temperature along with three control bottles containing no animals. On the May cruise the surface water used at stations 11 and 8 was filtered; in all following experiments unfiltered surface water was used. Samples for dissolved oxygen, ammonia, urea, and phosphate were taken at the beginning of the incubation period from the surface water that was used and from the experimental bottles after each incubation. Initially, these samples were just siphoned through a 10-μm mesh; however, phosphate levels can be increased by the particulate matter in the water. Therefore, on the August cruise the samples for nutrients were filtered through glass fiber filters. Consequently, phosphate samples at station 3 in May, November, and March may overestimate the amount of phosphate excretion, giving lower N:P ratios. Finally, after taking water samples, the animals were collected onto preweighed filters for dry weight determination as above.

General Circulation

Within 450 km of the coast of Nova Scotia three distinctly different oceanographic regions are found. Proceeding outward one passes successively through coastal water, Slope Water, and finally the Gulf Stream. Figure 1 shows the general circulation of this region based on the recent summary of Sutcliffe et al. (1976a).

Coastal water, here represented by the Nova Scotia current, is characteristic of the surface waters of the shelf. It possesses salinities that generally increase from 30 to 33‰ in an outbound direction. Perhaps the most characteristic feature of this region is that it is vertically separated into three distinct layers (Fig. 2). In addition to low salinities, the upper mixed layer (0–50 m) possesses the lowest surface temperatures on the transect. These, of course, change seasonally. The intermediate layer (50–150 m) is represented for most of the year as a region of minimum temperatures, usually <5°C. It originates in the northeast (Hachey 1938) and represents one branch of the southward flowing Labrador Current. This water mass is analgous to the "winter water" commonly observed off the middle Atlantic states (Ketchum and Keen 1955). The deepest layer (>150 m) is warmer and more saline than the intermediate layer and is only present beyond the outer banks or in the deepest

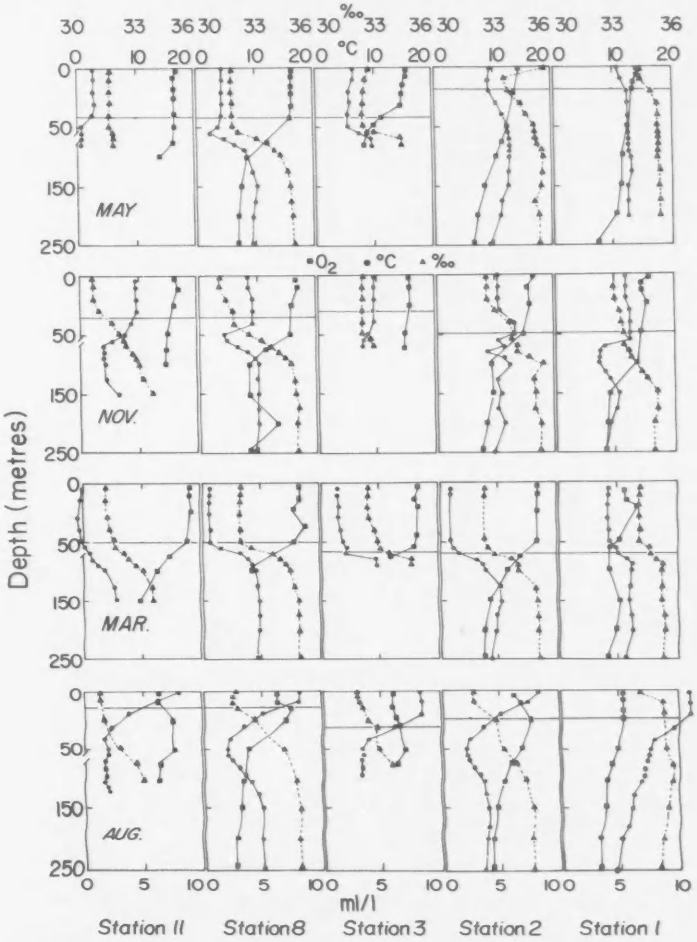

FIG. 2. Salinity (‰), temperature (°C), and oxygen (ml·litre^{-1}) profiles for each cruise from the major stations on the transect. Solid horizontal line is depth of euphotic zone.

areas of the shelf, such as Emerald Basin. Examination of Fig. 2 will show this layer most pronounced in the temperature profiles.

The drift of the Nova Scotia current has been put between 3.8–14.4 cm/s by drift bottle recoveries (Bumpus and Lauzier 1965), oil spill tracking (Forrester 1971) and seasonal temperature observations (Sutcliffe et al. 1976a). A value of 9 cm/s is a reasonable average. In addition, a definite offshore flow exists that has never been quantified (Trites and Banks 1958). Beyond the coastal water is the Slope Water defined by Iselin (1936) as "the bank of water between the edge of the continental shelf and the Gulf Stream". Although the boundary between coastal and Slope Waters is frequently in the vicinity of the shelf break, oceanographic rather than topographic criteria are more reliable indicators. McLellan et al. (1953) suggest that this boundary is encountered when a sharp increase in temperature occurs and isotherms become almost vertical, the three-layered coastal regime is lost and salinities generally increase to over 34.5‰. This transition can occur over a distance of 3.5 km or less. The shallow Slope Water represents an area of mixing and as such its salinities and temperatures (Fig. 2) are intermediate between those of coastal water and the Gulf Stream. The Slope Water ends when isotherms bend sharply downward indicating a rapid increase in temperature upon intersecting the Gulf Stream.

Although the exact nature of the circulation of the

TABLE 1. Chlorophyll *a* (milligrams per square metre) and adenosine triphosphate (milligrams per square metre) integrated over the euphotic zone at each station. Carbon values used in the carbon:chlorophyll ratios are calculated as 250 times ATP.

	May			Nov.	Mar.			Aug.			$\bar{x}$	
Stn.	Chl	ATP	C/Chl	Chl	Chl	ATP	C/Chl	Chl	ATP	C/Chl	Chl	ATP
12	29.5	—	—	58.0	17.4	1.8	25.9	6.9	3.3	119.6	25.7	2.6
11	17.1	4.7	68.7	56.7	18.6	2.4	32.3	14.6	4.4	75.3	26.8	3.8
8	29.0	5.3	45.7	11.5	21.6	2.3	26.6	5.1	2.0	98.0	16.8	3.2
5	47.4	—	—	19.6	27.6	2.7	24.5	4.5	1.2	66.7	24.8	2.0
3	18.9	4.8	63.5	25.7	61.4	3.9	15.9	5.7	2.4	105.3	28.0	3.7
2	28.8	—	—	21.4	34.7	4.7	33.9	8.0	3.8	118.8	23.2	4.3
1	62.5	19.6	78.4	22.5	35.4	2.8	19.8	1.3	1.2	230.8	30.4	7.9
$\bar{x}$	32.0	8.6	64.1	30.8	31.0	2.9	25.6	6.6	2.6	116.4		

Slope Water is unknown there is strong evidence for a northeasterly flow. This may take the form of one or many currents (Fuglister 1951) moving at speeds of up to 3.5 cm/s (McLellan et al. 1953). There is even a suggestion of a countercurrent in this region (Rossby 1936) which has yet to be demonstrated.

Results

Biological Observations

Biomass — Integrated values of chlorophyll *a* and ATP (Table 1) for the euphotic zone generally covaried. In March and May the highest values occurred at the seaward end of the transect, while in August and November the inner stations were higher. The most important fact revealed by the data is that there is not a consistent decline in chlorophyll *a* and ATP in a seaward direction. In fact, the data frequently show trends to the contrary with highest values occurring in Slope Water. For the four cruises the inner stations (12–5) were averaged and compared with the three outermost (3–1), which yielded values for chlorophyll *a* of 23.5 and 27.2 mg·m^{-2} and 3.0 and 5.4 mg ATP·m^{-2}, respectively.

Seasonal variability in chlorophyll *a* concentrations was marked only in August when average values dropped to only 20% of those observed during the remainder of the year. Although average August ATP values are similar to those of March the seasonality of these data is difficult to consider when the results of one cruise are unavailable. The fact that chlorophyll and ATP do not always vary in a similar fashion should not be surprising since the carbon to chlorophyll *a* ratio is known to be seasonally variable (Eppley 1968). Although chlorophyll *a* values drop severely from March to August compared with no change in ATP, this apparent discrepancy is due to changes in the amount of protozoa in the euphotic zone. Table 3 presents average values for dry weight of protozoa from the upper 50 m of all stations on each cruise (Johansen 1976). These data, when corrected for the depth of the euphotic zone and converted to carbon, are compared in Table 2 with the ATP estimates of carbon from the same locations. In May and March the protozoa account, on the average, for 5–10% of the living carbon passing a 153-μm mesh. However, in August this fraction jumps to >30%, which means that the average carbon:chlorophyll ratio of 116.4 (Table 1), reduces to 80.1. In May and March the change is almost insignificant. Johansen (1976) felt that this increase in protozoa was due to the marked increase at that time of small phytoplankton (<25 μm) upon which they feed.

The continuous traces in relative fluorescence (Fig. 3) agree in principle with the integrated chlorophyll *a* values. The profiles show high values for relative fluorescence within 20–30 km of the coast but on three of the four cruises relative fluorescence was higher in the outer 90 km of the transect (i.e. at one of the three outer stations) than in the inshore region, sometimes by as much as a factor of three. The fluorescence data from the first cruise have been examined in detail and are the subject of additional analysis (Mackas and Kamykowski, Department of Oceanography, Dalhousie University, personal communication). These individuals have demonstrated increases in relative fluorescence correlated with a general increase in temperature, with approach to the 10°C isotherm, i.e. Slope Water, but most clearly with any sharp temperature gradient such as could be expected when passing through an oceanic front.

Fewer generalities can be made concerning the zooplankton data (Table 2) since in two of the four cruises (November and March) our nets were clogged in the Slope Water first with salps and later with large masses of colonial diatoms.

TABLE 2. Total living carbon (milligrams per square metre) passing through a 153-μm mesh estimated as 250 times ATP (ATP), microscopic estimate of carbon represented by Protozoa (PRO), and percent decrease in carbon:chlorophyll ratio when protozoan carbon has been subtracted (ΔC/Chl).

	May			Mar.			Aug.		
Stn.	ATP	PRO	ΔC/Chl (%)	ATP	PRO	ΔC/Chl (%)	ATP	PRO	ΔC/Chl (%)
12	—	—	—	450	70	15.8	825	204	24.7
11	1175	90	7.6	600	60	10.2	100	135.9	12.4
8	1325	82	6.1	575	65	11.3	500	87.3	17.4
5	—	—	—	675	70	10.6	—	—	—
3	1200	56	4.7	975	51	5.0	600	321	53.5
2	—	—	—	1175	99	8.6	—	—	—
1	4900	96	1.9	700	45	6.6	300	144	48.0
$\bar{x}$			5.1			9.7			31.2

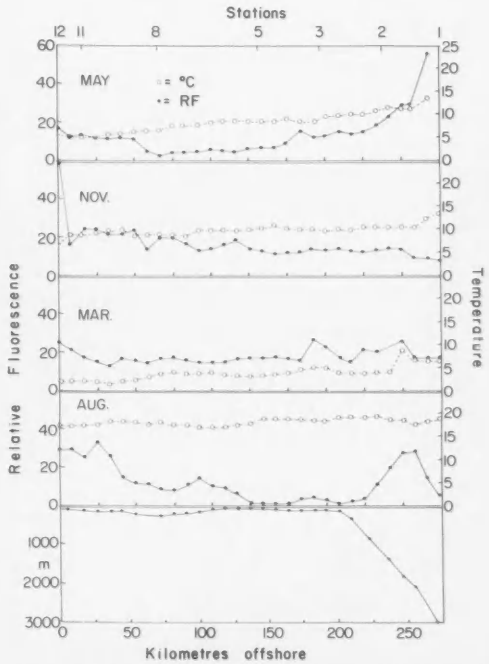

FIG. 3. Temperature and relative fluorescence plotted for each cruise along the length of the transect which begins in each case just outside Halifax Harbour. The bottom block shows the depth profile.

This precluded biomass estimates at these outer stations. On the two cruises when all stations were sampled, zooplankton biomass from stations 12–5, although quite variable, was decidedly higher than from stations 3–1 (40.5 and 18.8 $mg \cdot m^{-3}$ and 4.5 and 2.3 $g \cdot m^{-2}$, respectively).

The smallest zooplankters, the protozoa (Table 3), were generally <5 mg dry $wt \cdot m^{-3}$ in the upper 50 m of the water column (Johansen 1976). Higher values were observed at the outermost stations in May and November and the entire August transect. The latter cruise showed more than a threefold increase in protozoan biomass over the previous three cruises. This is consistent with the annual cycle observed in Halifax Harbour by Johansen (1976) which suggested that these animals are most abundant in late summer when the smallest phytoplankters are also abundant. Although mean station biomass declines from inshore to the outer edge of the shelf and then rises once again, stations 12–5 show a mean of 6.3 $mg \cdot m^{-3}$, while stations 3–1 show a marginal increase to 7.3 $mg \cdot m^{-3}$.

Primary production — Table 4 presents the primary production data integrated over six depths in the euphotic zone. The values obtained thus far when extrapolated to a full year yield an annual production of 265 mg $C/(m^2 \cdot day)$ or 96.6 g $C/(m^2 \cdot yr)$. Considering only stations 11–5 this becomes 181.2 mg $C/(m^2 \cdot day)$. The single most productive station was on Emerald Bank (No. 3) with a mean value of 349 mg $C/(m^2 \cdot day)$. Although each of the four seasons is represented no values are available for the spring flowering. There is little doubt that observations made during the spring flowering will significantly augment the observed annual level of production.

Table 4 also presents the photosynthetic index (P.I.) calculated as mg C m^{-3} h^{-1}/mg Chl *a* m^{-3} for each of the experimental depths from 100 to 1%. Then, from each set of six, the highest value was selected, usually from the 20% light level (Platt and Subba Rao 1973). This was done on the assumption that the highest values were

TABLE 3. Zooplankton dry weight (milligrams per cubic metre and grams per square metre) and Protozoa (milligrams dry weight per cubic metre) in the top 50 m of the water column (Johansen 1976).

	May			Nov.			Mar.			Aug.			$\bar{x}$		
Stn.	m^{-3}	m^{-2}	PRO	m^{-3}	m^{-2}	PRO	m^{-3}	m^{-2}	PRO	m^{-3}	m^{-2}	PRO	m^{-3}	m^{-2}	PRO
12	41	2.2	3.4	24.2	1.1	8.2	4.1	0.3	2.8	63.4	3.9	22.7	33.2	1.9	9.3
11	34	4.1	4.5	11.0	1.7	6.3	7.3	0.8	2.4	56.6	5.5	15.1	27.2	3.0	7.1
8	25	4.6	4.1	36.8	8.7	5.1	12.2	2.6	2.6	72.4	14.0	9.7	36.6	7.5	5.4
5	154	10.9	3.7	15.7	1.1	3.8	7.2	—	2.8	82.3	5.7	—	64.8	5.9	3.4
3	86	8.0	2.8	—[a]	—[a]	7.7	—[b]	—[b]	1.7	1.0	0.1	21.4	43.5	4.0	8.4
2	5	0.9	6.1	—[a]	—[a]	4.7	—[b]	—[b]	3.3	2.0	0.6	—	3.5	0.8	4.7
1	11	2.4	9.6	—[a]	—[a]	9.6	—[b]	—[b]	1.5	7.6	1.9	14.4	8.8	2.1	8.8
$\bar{x}$	50.9	4.7	4.9	21.9	3.2	6.5	7.7	1.2	2.4	40.8	29.7	16.7			

[a]Large quantities of salps. No biomass measured.
[b]Large quantities of colonial diatoms. No biomass measured because of net fouling.

TABLE 4. Primary productivity (milligrams of carbon per square metre per day) integrated over the euphotic zone and the productivity index (per hour) calculated as the ratio of light saturated uptake of carbon (milligrams of carbon per cubic metre per hour):chlorophyll *a* (milligrams per cubic metre) at the same depth.

	May		Nov.		Mar.		Aug.	
Stn.	Prod.	P.I.	Prod.	P.I.	Prod.	P.I.	Prod.	P.I.
11	126	1.6	—	—	—	—	—	—
8	136	2.2	462	6.3	123	0.7	181.3	4.9
5	—	—	117	6.8	—	—	—	—
3	228	3.5	—	—	612	1.3	206.2	8.8
2	—	—	—	—	—	—	270.2	5.5
1	466	13.7	531	2.8	42.3	0.5	104.7	6.0

closest to light saturation, which then allowed comparisons between stations and cruises. Caperon et al. (1971) have suggested that the photosynthetic index can be used as an index of nutrient availability. Under otherwise similar conditions phytoplankton in contact with higher concentrations of available nutrients will yield higher indices. The highest P.I. observed (13.7) occurred in Slope Water in May at the end of a steady seaward gradient. In August high values (5.5–8.0) once again occurred at the outer end of the transect but this distinction was not as pronounced as on the earlier cruise. In November the highest values were observed on the shelf, while March was generally low (0.5–1.2) with no pattern whatever. These values when averaged for stations 12–5 and 3–1 yield 3.8 and 5.3 h^{-1}, respectively.

One further calculation is possible using the productivity and biomass data. Table 5 presents an experimental estimate of the maximum growth rate (μ) in doublings per day calculated as $\mu = 3.32 \log_{10} C_{t+1}/C_t$ (Eppley et al. 1973). In addition, the maximum potential growth rate was calculated using the equation of Eppley (1972) $\log_{10} \mu = 0.0275T - 0.07$ where T = the temperature of the mixed layer in degrees Celsius. Since this latter equation yields a growth rate for a 24-h growing period, the values obtained were halved to allow comparison with the experimental data.

The growth rates in Table 5 vary by as much as threefold on any single cruise but they show one consistent trend. The maximum value observed on any transect occurred at station 3, which is located closest to the shelf break. In each case, the value observed there is markedly higher than any others. Since the calculation of μ is a ratio of standing crop plus daily carbon augmentation to standing crop alone, these very high values indicate a relatively higher production per unit biomass than anywhere else on the transect. The amount of standing crop that is present, whether high or low, is immaterial. This can be verified by examination of Fig. 3 and Table 1. Temperature alone is not responsible as can be seen in Table 5 where temperatures continue to rise at stations 2 and 1 while the growth

TABLE 5. Experimental (Exp) and expected maximum growth rates (Max). The experimental rates were calculated using carbon (250 times ATP, corrected for Protozoa), and primary productivity values from the depth of maximum production at each station, while the theoretical value was based on the temperature (degrees Celsius) of the mixed layer (see text for details).

	May			Mar.			Aug.		
Stn.	Temp	Exp	Max	Temp	Exp	Max	Temp	Exp	Max
11	3	0.94	0.52	—	—	—	—	—	—
8	4	0.78	0.55	1	0.39	0.45	16	0.89	1.17
3	6	1.44	0.62	3	1.03	0.52	17	1.66	1.25
2	—	—	—	—	—	—	16	0.77	1.17
1	11	0.59	0.85	8	0.62	0.70	22	0.64	1.71

rates decline. Averaging, as previously, yields 0.75 and 0.96 doublings·day^{-1} for the inshore and offshore stations, respectively.

An interesting feature of these data is the fact that five of the experimental estimates are higher than the expected maximum (Eppley 1972). Three of these occur at station 3, while the others are inshore in May. The expected maximum can apparently be exceeded whenever ideal environmental conditions are achieved as seems to regularly occur in the region of the shelf break.

Zooplankton excretion — Zooplankton respiration and excretion rates are reasonably similar (Table 6) when seasonal differences in temperature, species composition, and biomass are accounted for. Thus, the November and August rates are higher than May and March. However, the difference between stations 8 and 1 in August is almost certainly due to the different species composition — *Calanus finmarchicus* at station 8 and *Pleuromamma sp.* at station 1. In addition to the seasonal variation there was some diel variation, averaged out in Table 6, due to differences in species composition of the surface waters and differences in activity of the zooplankton during the day. Excretion data, expressed as nanogram-atoms per litre per day, averaged for the euphotic zone (Table 7) includes differences in biomass between stations and within a daily cycle. Thus, the great difference seen in August between stations 8 and 1, representing the shelf and slope, respectively, is the opposite of the weight specific rates shown in Table 6 because of the much higher zooplankton abundance on the shelf.

Coupling total zooplankton excretion with phytoplankton nitrogen and phosphorus requirements estimated from ^{14}C uptake and then converted using a C:N:P ratio of 106:16:1 (by atoms) (Redfield et al. 1963) provides a measure (Table 7) of the importance of zooplankton cycling to phytoplankton growth. The zooplankton supplied a mean of 22% (range 2–50%) of the nitrogen required for the observed phytoplankton growth. With regard to phosphorus the mean was 41% with a range of 4–75%. At station 8, which was the only station sampled in all four seasons, the highest percentages were recorded during the late spring and summer, while the lowest occurred in the fall and winter.

TABLE 6. Zooplankton excretion of nitrogen and phosphorus [(ng-at (mg · hr))] and respiration [(μg-at O_2 × 10^{-2} (mg · hr))] plus the temperature of incubation (°C). These values are the averages of four experiments conducted during the day. We intended to repeat these observations at the same stations on each cruise. However, time limitations and problems encountered in collecting sufficient crustacean zooplankton for the experiments (salps were not used) made this impossible. Station 8 is represented on all four cruises, and stations 5 and 3 are hydrographically similar; but the only experiment done in Slope Water was done at station 1 in August.

	Stn.	Temp	O_2	NH_3	Urea	PO_4	Total N / P
May	11	2	11.1	10.3	3.4	1.3	10.7
	8	3	10.5	8.2	1.7	0.9	4.0
	3	5	14.2	8.1	3.1	1.6	7.0
Nov.	8	8	31.5	17.3	1.1	4.5	4.1
	5	9	36.6	24.0	2.1	3.5	7.5
Mar.	8	3	13.0	8.5	0.5	2.1	4.3
	5[a]	3	14.4	13.0	0.0	2.3	7.3
Aug.	8	17	21.3	18.5	0.0	1.6	11.6
	1	21	83.0	31.4	4.6	5.2	6.9
$\bar{x}$			26.2	15.5	1.8	2.6	7.8

[a]Number is based on only one experimental observation, obtained at night at this station.

Nutrients — Although we have data for each station and cruise for nitrate, ammonia, urea, phosphate, nitrite, and silicate, only nitrate and phosphate will be presented in their entirety (Fig.

TABLE 7. Coupling of zooplankton excretion (nanogram-atoms per litre per day) and phytoplankton assimilation (nanogram-atoms per litre per day) expressed as a ratio.

		ZP excretion		PP assimilation		Excret:assim	
		N	P	N	P	N	P
May	11	16.0	1.5	31.7	2.0	0.50	0.75
	8	17.3	1.5	40.6	2.5	0.43	0.60
	3	16.2	2.2	68.2	4.3	0.24	0.51
Nov.	8	9.7	2.2	171.1	10.7	0.06	0.21
	5	13.3	1.8	49.3	3.1	0.27	0.58
Mar.	8	2.2	0.5	31.6	2.0	0.07	0.25
	5	2.3	0.3	132.7	8.3	0.02	0.04
Aug.	8	45.8	4.1	151.9	9.5	0.30	0.43
	1	7.3	1.1	57.2	3.5	0.13	0.31
$\bar{x}$		14.5	1.7	81.6	5.1	0.22	0.41

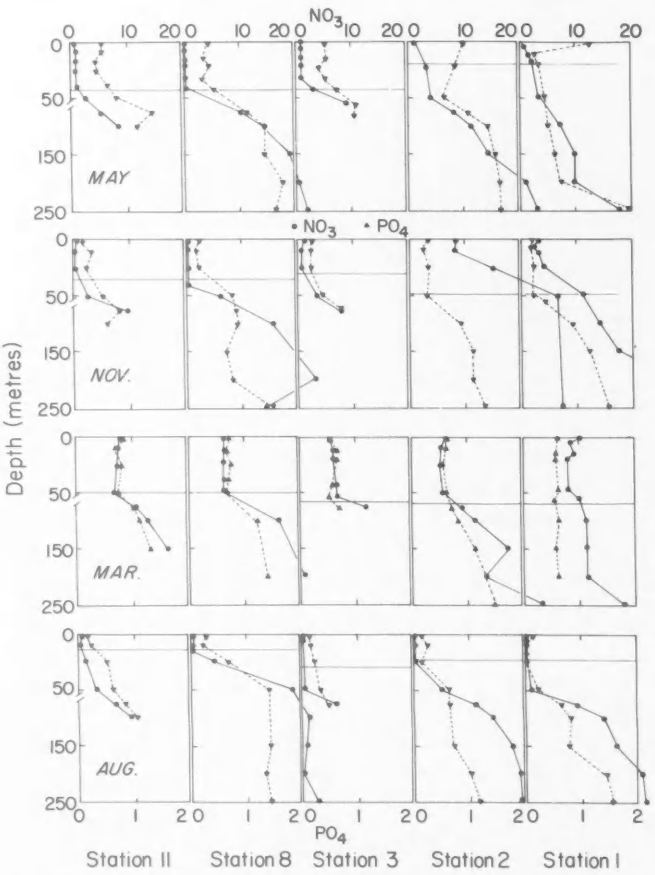

FIG. 4. Nitrate and phosphate profiles (μg-at·litre^{-1}) for each cruise from the major stations on the transect. Solid horizontal line is depth of euphotic zone.

TABLE 8. Ratio of nitrate to phosphorus in the euphotic zone, between 50 and 100 m and at 50-m intervals are presented in the first column where total nitrogen (nitrate, nitrite, urea and ammonia) to phosphorus in the second.

	11		8		3		2		1	
May										
EZ	1.8	3.2	0.7	2.2	2.2	3.4	2.8	3.3	2.9	5.6
50–100	5.2	6.2	9.9	10.8	12.7	13.1	7.8	8.1	11.0	12.8
150	—	—	13.4	13.6	—	—	9.4	9.6	15.4	15.7
200	—	—	11.7	12.1	—	—	12.9	13.2	13.7	14.0
250	—	—	13.8	14.1	—	—	14.0	14.3	9.4	9.5
Nov.										
EZ	0.8	5.8	0.2	2.5	3.7	5.3	31.8	33.6	21.7	25.9
50–100	9.8	11.9	12.4	13.3	9.3	9.9	—	—	14.7	20.7
150	—	—	5.4	—	—	—	4.0	5.7	14.3	15.4
200	—	—	26.3	26.9	—	—	—	—	—	—
250	—	—	9.2	9.9	—	—	19.8	20.3	20.5	21.3
Mar.										
EZ	9.4	10.4	9.2	10.5	11.0	11.8	9.3	9.6[a]	15.0	15.8
50–100	10.8	11.0	12.9	13.3	16.7	17.4	13.1	13.2[a]	17.4	18.5
150	12.1	12.4	—	—	—	—	15.7	15.7[a]	19.0	19.7
200	—	—	14.8	15.4	—	—	10.0	10.1[a]	18.5	19.2
250	—	—	—	—	—	—	15.7	15.8[a]	16.4	18.5
Aug.										
EZ	0.1	2.8	0.2	2.6	0.1	3.0	0.1	1.8	0.2	4.7
50–100	7.7	6.5	14.1	14.5	7.5	9.2	15.7	16.3	13.8	14.6
150	—	—	14.7	14.9	—	—	25.0	25.6	20.5	21.7
200	—	—	14.9	16.0	—	—	18.5	18.9	14.5	14.9
250	—	—	15.7	16.0	—	—	16.2	16.6	14.0	13.9

[a] NH_3 and urea not available for these samples.

4). The silicate data covary with nitrate so that little insight is gained by presenting both. The nitrate data from the November cruise are presented but they are suspect because of exceptionally high values. We are not certain but we feel that the Whirlpak® bags used to contain the samples on that trip may have permitted contamination during freezing and subsequent transportation.

Nitrate concentrations in the euphotic zone follow a pattern common to east coast temperate continental shelves (Ketchum et al. 1958). In May following the spring flowering, concentrations were low (0.5–1.5 μM) but not as low as in August when minimum values for the year (<0.5 μM) were recorded. In November the values were intermediate (0.5–4 μM), while in March the highs for the year (7.5–10 μM) were observed. In addition to these seasonal changes, a slight but gradual increasing trend is visible in an offshore direction. And lastly, a vertical trend is also visible. Below the euphotic zone nitrate values increase sharply at all stations but they do not all rise in a similar fashion. In Emerald Basin (Station 8), nitrate values vary between 5 and 20 μM between 50 and 100 m. Other stations at similar depths vary between only 2.5 and 12 μM.

Nitrogen:phosphorus ratios (Table 8) were calculated in two ways: as either total nitrogen (i.e., nitrate, nitrite, ammonia, and urea) or as nitrate alone. The first calculation permits an estimate of the total quantity of nutrients available to the algae, while the second permits some consideration of possible mechanisms of transport (Riley 1967), such as advection. In the latter case nitrate is used as a semiconservative property because of its very long regeneration time (Ryther and Dunstan 1971) compared to phosphorus and the other nitrogenous nutrients. The difference between the ratios reflects the relative importance of new and recycled nitrogen. The nitrate:phosphorus ratios for the euphotic zone averaged for stations 12–5 and 3–1 were 3.6 and 4.8, respectively, while from 50 to 100 m they were 10.1 and 12.9, respectively.

Discussion

The classical explanation for the fertility of continental shelves is that land-derived nutrients are the major enriching mechanism. Ketchum and Keen (1955) attempted to quantify this input for a large segment of the east coast of North America and concluded that the supply was in-

sufficient to meet the annual phytoplankton requirements. Thus, this explanation has been relegated to a minor role (Riley 1967). Despite this, most transects run normal to the coast usually show a gradual decline in biological activity with increasing distance from land (Ketchum et al. 1958; Ryther and Yentsch 1958; Haines and Dunstan 1975). The Scotian Shelf is apparently unique among these studies in that just the reverse is true.

Table 9 presents a summary of the variables measured on the four cruises expressed as means for those stations clearly representative of the shelf (12–5) and those characteristic of the shelf–slope boundary (3–1). These data show no decline with passage offshore but rather they are constant or show a sharp increase in the shelf–slope region. The only exceptions are macrozooplankton collections, which invariably declined at the outermost three stations. Recent attempts to tow at depths in excess of 300 m have not reversed this trend. Collections to the south by Clarke (1940) and Grice and Hart (1962) have shown relatively higher concentrations of zooplankton in the shelf–slope region. The sharp decline in our data must remain unexplained for the present.

The reason for enhanced biological activity in the shelf–slope region is not known but may be due to higher nutrient concentrations resulting from increased vertical turbulence. During May and August the average concentration of nitrate at station 2 between 50 and 100 m is approximately 10 μM. Evidence for increased nutrient input into the euphotic zone is visible in Fig. 4 and Table 8. In the former, nitrate and phosphate concentrations increase slightly in a seaward direction along the transect. In the latter case the nitrogen:phosphorus ratios indicate an increase in the euphotic zone of the last three stations of approximately 20% over the inshore stations.

TABLE 9. An inshore:offshore comparison of the variables measured on four cruises. A demonstration of statistical significance has not been attempted (because of wide seasonal variability) nor is any implied.

	Stations	
	12–5	3–1
Chlorophyll ($mg \cdot m^{-2}$)	23.5	27.2
ATP ($mg \cdot m^{-2}$)	3.0	5.4
Prim. prod. ($mg\ C/(m^2 \cdot day)$)	181.2	349.7
Growth rate (doublings day^{-1})	0.75	0.96
Prod. index (h^{-1})	3.8	5.3
Protozoa ($mg \cdot m^{-3}$)	6.3	7.3
Zooplankton ($mg \cdot m^{-3}$)	40.5	18.8
Zooplankton ($mg \cdot m^{-2}$)	4466	2306
$NO_3:PO_4$ *(euphotic zone)*	3.6	4.8
$NO_3:PO_4$ (50–100 m)	10.1	12.9

The physical explanation for increased vertical mixing in this area is poorly understood. We feel that the sharp temperature gradients frequently encountered in this region identify fronts that are regions of strong mixing. What is not clear is how the compromise between upward moving nutrients and downward moving phytoplankton is reached so that production can occur in the lighted layers. Pingree et al. (1975), working with a tidally mixed front in the English Channel, have suggested that mixing followed by relaxation can occur. In any case, the sharpest front, signifying the boundary between coastal and Slope Water, is the most enduring and hence probably the most important biologically. Satellite infrared photographs (E.R.O.S. Data Center, Sioux Falls, S.Dak.) and hydrographic surveys (McLellan et al. 1953) of this area indicate that the geographic location of the front is quite variable over a time scale of days to weeks. Figure 3 shows maximum chlorophyll fluorescence in May, March, and August occurring within a 90 km area roughly equivalent to stations 3–1. Hence vertical mixing accompanying the shelf–slope front and the resultant increase in biological activity may vary spatially on the order of tens of kilometres enriching the shelf–slope boundary region relative to the shelf proper.

Any contemporary discussion of the reasons for continental shelf productivity ultimately settles on the supply of limiting nutrients. In most marine cases, and the Scotian Shelf is no exception, the single most important nutrient is nitrogen. The nitrogen reaching the phytoplankton is usually in one of several forms and the route followed by each can be quite varied. New additions to the system can occur through rain, runoff, or nitrogen fixation, while old nitrogen can be regenerated in place or elsewhere followed by advection or diffusion to the point of utilization. In most areas all of these factors undoubtedly contribute to some degree but it is unlikely that their contributions are ever equal. For the present we wish to assign the collective regeneration input to the shelf at 80% of the annual phytoplankton requirements. Nutrient regeneration is continually underway by all the planktonic, nektonic, and benthic animals plus bacteria. We have shown the zooplankton to account for an average 20% of the annual phytoplankton nitrogen requirements. Rowe et al. (1975) have suggested that the benthos alone may on occasion account for more than 100%. Since the Scotian Shelf is not a

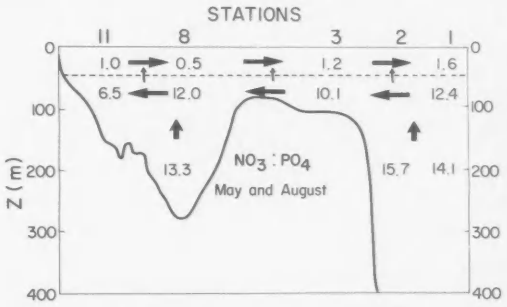

FIG. 5. Nitrate:phosphate ratios averaged for May and August from the euphotic zone (above dashed line) and 50–100 m depth zones. In addition values were calculated at 200 m for three stations.

closed system it seems unlikely that the average annual benthic contribution would be 100%. We feel that a value of 80% is reasonable and conservative for the sake of the following discussion. At any rate variation of ±20% about the value would not materially alter our conclusion.

Previously the existence of several potential sources of new nitrogen were alluded to. At this time only one will be considered: the nitrate-rich Slope Water. However, before doing so, it should be pointed out that the outflow from the Gulf of St. Lawrence annually contributes about 1% of the volume of the waters over the shelf (Trites 1970). This water passing through the Cabot Strait is concentrated in the upper 50 m (Sutcliffe et al. 1976a) and thought to be nutrient poor (Steven 1974).

Riley (1967) was the first to suggest that the Slope Water might be a potentially important source of enrichment for continental shelves. He argued that evidence for his proposed steady-state diffusive model could frequently be seen in the form of a gradient in NO_3:PO_4 ratios normal to the coast. The underlying assumption here is that phosphorus is recycled rapidly on the order of days, while nitrate is returned to the water over a period of months. Hence, nitrate in this instance can be used as a semiconservative property and increasing gradients in NO_3:PO_4 can reflect potential sources of enrichment.

Figure 5 shows nitrate:phosphate ratios averaged for the euphotic zone and for 50–100 m at five stations. These data include only the spring and summer cruises and are generally indicative of the period following the spring flowering to the period just prior to the initiation of fall mixing. The euphotic zone and 50–100 m layer show increasing gradients in a seaward direction. Station 8 (Emerald Basin) shows values that are slightly anomalous because it is not dependent on cross-shelf transfer for enrichment. Emerald Basin has access to Slope Water through a channel (Scotian Gulf) about 70 km south of Station 3 at a depth of about 160 m (i.e. 70 m deeper than the surrounding shelf). Current measurements in this channel (Warner 1970) have shown on occasion a pulsing inflow at 130 m and a strong outflow at 50 m. Warner (1970) has also shown that the Scotian Shelf south of Halifax was characterized by high internal wave activity and strong tidal fluctuations. If some of this energy were propagated from the shelf break through the Scotian Gulf into Emerald Basin this would undoubtedly result in some vertical mixing and enrichment of the upper layers independent of the rest of the shelf. In general then the NO_3:PO_4 gradients above and below the euphotic zone lend support to Riley's (1967) hypothesis. Deep nutrient-rich water may move onto the shelf where its contents would be mixed upward either gradually or sporadically and utilized in primary production.

For this mechanism to work it must be able to realistically satisfy the nitrogen requirements of the phytoplankton on the shelf. During the period April to September at least 50% of the annual production occurs, which in this case is 50 g $C \cdot m^{-2}$. This value is almost surely an underestimate since production values have not yet been obtained during the spring flowering. Further measurements could augment it by 50%. Assuming for the present that 50 g $C \cdot m^{-2}$ (4.16 g-at $C \cdot m^{-2}$) are being fixed in this period, this is equivalent (using a C:N ratio of 6.6:1 by atoms) to an uptake of 0.63 g-at $N \cdot m^{-2}$. Assuming that 80% of the required nitrogen is being recycled, then 20% or 0.13 g-at $\cdot m^{-2}$, must be supplied new. Figure 6 displays a hypothetical 1-cm-wide channel, 100 m high and 188 km long. To supply 0.13 g-at $N \cdot m^{-2}$ over the length of the transect

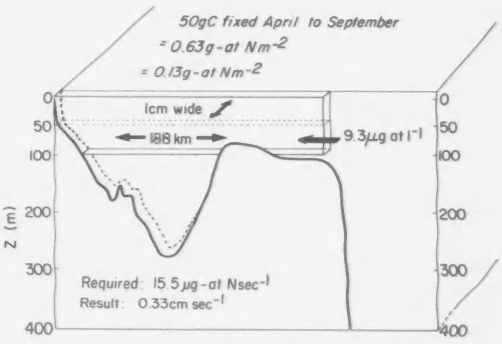

FIG. 6. A hypothetical 1-cm-wide, 188-km-long box along which Slope Water might move onto shelf.

between April and September requires an input of 15.5 μg-at $N \cdot s^{-1}$. Using the average value of 9.3 μg-at $NO_3^- \cdot \ell^{-1}$ between 50 and 100 m at Station 2 yields an average value of 0.33 $cm \cdot s^{-1}$.

Riley's (1967) original model proposed this as diffusive rather than advective transfer. Although diffusion may be important in some areas it seems more likely when considering the dynamics of the Scotian Shelf, that the transfer is advective. Platt et al. (1972) and Heath (1973) have suggested that a similar mechanism accounts for the transfer of nutrient-rich shelf water into east coast Nova Scotia embayments. Advection at the rate of 0.33 $cm \cdot s^{-1}$ is quite small especially when compared to an average long shore drift of approximately 10 $cm \cdot s^{-1}$. The value of 0.33 $cm \cdot s^{-1}$ is the required average flow which can be achieved just as well by a series of sporadic events, such as storm surges, which move large quantities of water at irregular intervals.

The sporadic intrusion of Slope Water onto the shelf is well documented. The first evidence showed flooding of the southwestern shelf in the summer of 1934 (Liem and Hachey 1935). Later observations showed similar intrusions into the Scotian Shelf in winter (Hachey 1953) and along the same section described in this paper in 1950 (McLellan and Trites unpublished data; McLellan et al. 1953). The authors in the latter case suggested that this may have resulted from the passage of a tropical storm along the coast just before their cruise. In general, there is a persistence to these incursions which suggest that they are characteristic of the circulation of the Scotian Shelf.

At this point we would like to consider several mechanisms both continuous and sporadic, which might possibly promote this crosscurrent transfer of Slope Water. The first approach is to consider coastal waters as analogous to a large estuary (Yentsch 1975). Land-derived freshwater enters and mixes with coastal waters and gradually moves offshore as evidenced by salinity gradients. Although the input of freshwater is small, the resultant flow can be large due to entrainment. Thus, a two-layered flow would exist with offshore transport in the surface layers and compensating return flow below. The return flow would be higher in nutrients and through the process of entrainment would enrich the upper layers. The major source of freshwater to the Scotian Shelf is the St. Lawrence River which delivers on an annual basis approximately 1% of the volume of water overlaying the shelf (Trites 1970). This river is highly seasonal with maximum overflow recorded in the Cabot Strait during September and October (Sutcliffe et al. 1976a). Although an estuarine circulation remains a possible mechanism, it is the least likely for the reasons stated by Ketchum and Keen (1955) and Riley (1967).

The second mechanism considers the apparent relationship between prevailing winds and offshore surface flow. Hachey (1937) examined wind and sea–surface temperature taken over an 8-yr period which suggested that changes in temperature in Halifax Harbour could be explained as a result of wind driven Ekman circulation of surface water offshore. A more recent study off Maryland (Boicourt and Hacker 1975) showed an offshore Ekman drift which resulted from a prevailing southerly wind. Their observations clearly demonstrated the presence of a compensating return flow.

The final mechanism would occur as a direct result of the irregular northern boundary of the Gulf Stream south of the Scotian Shelf. This boundary as seen from infrared satellite photographs or short-term hydrographic surveys (McLellan 1957) is irregular and somewhat undulating. Some of the effects attributed to the lateral movement of this boundary are marked rapid changes in the position of fronts plus drastic changes in the width of the Slope Water of anywhere from 20 to 270 km (McLellan et al. 1953). Assuming this boundary was coherent to depths of 100 m then an irregular, low frequency forcing may produce subsurface intrusions on the shelf of nutrient-rich Slope Water. In the final analysis a decision as to which of the above mechanisms, if any, is dominant must await improved physical oceanographic data.

Acknowledgments

We are deeply indebted to a large number of students from the Department of Oceanography too numerous to name who voluntarily contributed a great deal of time and effort to the success of this program. In addition we are grateful to Dr D. Kamykowski and Mr D. Mackas for providing us with their continuous chlorophyll data, to Dr E. Anderson for his assistance with the initial zooplankton regeneration experiment, to Dr P. Johansen for assistance with the microzooplankton analyses and to Miss E. Todd for her painstaking care with various chemical analyses.

Thanks also go to the captain, officers and crew of C.S.S. *Dawson*. In addition we have benefited immeasurably from frequent conversations with Dr G. A. Riley.

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White Sucker (*Catostomus commersoni*) Embryo Development, and Early Growth and Survival at Different Temperatures

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McCormick, J. H., B. R. Jones, and K. E. F. Hokanson. 1977. White sucker (*Catostomus commersoni*) embryo development, and early growth and survival at different temperatures. J. Fish. Res. Board Can. 34: 1019–1025.

White suckers (*Catostomus commersoni*) were exposed from fertilization through hatching to seven constant temperatures from 6.2 through 24.1°C. High percentages of apparently normal larvae hatched at temperatures from 9.0 through 17.2°C. Maximum percent hatch occurred at 15.2°C, while only a few normal larvae were produced at 6.2°C, and none at 24.1°C.

Growth rates increased from near zero at 10.0°C to a maximum at 26.9°C. At 29.7°C growth fell below the maximum ($P < 0.05$), and the incidence of spinal deformities was high. Death rates were uniformly low from 15.7 to 26.9°C and were significantly higher at 10.0 and 29.7°C ($P < 0.05$). The rate of net biomass gain for test groups was maximum at 26.9°C. Net rates of biomass gain declined progressively with temperatures below 26.9°C until by 10.0°C the rate of population growth became less than the rate of weight loss through deaths within the population. The temperature producing maximum hatching success, 15°C, was nearly 12°C lower than that providing for maximum growth and net biomass gain.

Upper thermal 1-, 2-, and 7-day TL50 values for both newly hatched and swim-up larvae, when acclimated to 9 and 10°C, were between 28 and 29°C. When acclimated to 15 and 21°C, they were between 30 and 32°C.

Lower 1-day TL50 temperature values for both groups of larvae acclimated to 21°C were near 3°C (<2.9), 2-day TL50 values were approximately 0.5°C higher, and 7-day values were 4.8°C for newly hatched larvae and 6.1°C for swim-up larvae.

McCormick, J. H., B. R. Jones, and K. E. F. Hokanson. 1977. White sucker (*Catostomus commersoni*) embryo development, and early growth and survival at different temperatures. J. Fish. Res. Board Can. 34: 1019–1025.

Nous avons exposé, depuis la fécondation jusqu'à l'éclosion, des embryons de meunier noir à sept températures constantes allant de 6.2 à 24.1°C. De forts pourcentages de larves « normales » éclosent à des températures de 9.0 à 17.2°C. Le maximum d'éclosion se produit à 15.2°C, mais seulement quelques larves « normales » éclosent à 6.2°C et aucune à 24.1°C.

Les rythmes de croissance augmentent avec des températures successivement plus élevées, de près de zéro à 10.0°C à un maximum à 26.9°C. A 29.7°C, la croissance tombe au-dessous du maximum ($P < 0.05$), et il se développe chez les larves une forte incidence de difformités de l'épine dorsale. Les taux de mortalité sont uniformément bas entre 15.7 et 26.9°C et sont nettement plus élevés à 10.0 et 29.7°C ($P < 0.05$). Les taux de gain net de biomasse sont à leur maximum à 26.9°C. Ils diminuent à des températures décroissantes au-dessous de 26.9°C, jusqu'à ce que, à 10.0°C, le taux de croissance de la population est moindre que le taux de perte de poids par mortalité. La température produisant la meilleure éclosion, 15°C, est presque de 12°C inférieure à celle qui produit un maximum de croissance et de gain net de biomasse. Les valeurs supérieures de la TL50 après 1,2 et 7 jours, tant pour les larves nouvellement écloses que pour celles qui nagent vers le haut, acclimatées à 9 et 10°C, se situent entre 28 et 29°C. Lorsque acclimatées à 15 et 21°C, les larves des deux groupes d'âge ont des TL50 après 1, 2 et 7 jours allant de 30 à 32°C. Les valeurs inférieures de la TL50 après 1 jour pour les deux groupes de larves acclimatées à 21°C se rapprochent de 3°C (<2.9). Les TL50 après 2 jours sont d'environ 0.5°C plus élevées, et les valeurs après 7 jours sont de 4.8°C pour les larves nouvellement écloses et 6.1°C pour les larves nageant vers le haut.

Received August 8, 1975
Accepted March 18, 1977

Reçu le 8 août 1975
Accepté le 18 mars 1977

Printed in Canada (J3944)
Imprimé au Canada (J3944)

This report provides thermal response data for embryos of the white sucker (*Catostomus commersoni*) tolerance limits for the previously unstudied newly hatched and swim-up stages, and growth and mortality responses during their first weeks of life. Such data are essential in estimating the effects that various thermal regimes may have on the well-being of white suckers during these critical early life stages, as well as to help predict the course of interactions with fishes of natural communities.

Temperature requirements for some life stages of the white sucker have been determined previously. Raney and Webster (1942) and Raney (1943) report spawning runs from April to June, starting as temperatures reach 7.2°C, and peaks at 17.8°C. Information on adults indicates a preferred temperature of 19–21°C (Horak and Tanner 1964) and an ultimate upper lethal temperature of 29.3°C (Hart 1947). Work with juveniles has shown the upper 12-h TL50 to be 31.2°C when acclimated at 25°C (Brett 1944) and the lower 24-h TL50 to be 2.5 and 6.0°C when acclimated at 20 and 25°C, respectively (Hart 1947). Raney and Webster (1942) investigated the temperature tolerance of embryos, but only to determine broad limits.

Materials and Methods

Mature white suckers were collected from Greenwood Lake, Cook County, Minnesota, and transported to the Environmental Research Laboratory-Duluth where the eggs were removed and fertilized using the dry fertilization technique. Laboratory fertilization was employed to insure exposure of the embryos at the sensitive stages early in development (Hokanson et al. 1973a).

Test temperatures were maintained by a continuous flow of water at constant temperatures (McCormick and Syrett 1970). Flow rates through all exposure units were 200–250 ml/min. Test temperatures were monitored with recording telethermometers which were calibrated daily with a mercury thermometer to the nearest 0.1°C. Temperatures reported are the means of once-daily thermometer readings except when temperature deviations exceeded 1.0°C for more than an hour, when a daily mean was calculated from the temperature recording chart. Embryo responses to test temperatures were evaluated in 1968 and 1969, three replicates in 1968 and two in 1969. Testing at 12°C, added in 1969, resulted in only two replicates at that temperature. Temperatures used in the analysis were the grand means of both years.

Test water in 1968 was carbon-filtered Lake Superior water previously treated for Duluth, Minnesota, domestic use. Carbon filtration reduced the chlorine and chloramines to a mean of 4 μg/liter, ranging from 1 to 10 μg/liter. In 1969 Lake Superior water pumped directly from the lake became available and was used. Because the results in the 2 yr were not statistically different ($P>0.05$, t-test), the data from both years were treated together.

Embryo Survival

Treatments ranged in temperature from 6 through 24°C. Embryos from different pairs of adults were used for each of the five tests: A, B, C, D, and E (Table 1). Subsamples of embryos from each pair were randomly assigned to treatments within each replicate. In 1968 embryos were exposed directly to the test temperatures after dry fertilization without tempering or water hardening. In 1969 exposures were started with tempering at the rate of 3°C/h. To expedite placement of the embryos into test temperatures early in development, embryo sample size was first determined by volume. Enumeration followed at a less critical time. Sample sizes were lots of 100 or more except for 80 at 17.5°C, replicate D, and 97 at 9°C, replicate D. Embryos were incubated according to standard hatchery-jar procedure in 1968, but in 1969 were supported on stainless steel screens above a turbulent water discharge at the bottom of each jar (McCormick and Syrett 1970). Again, treatment effects between years were not detected ($P>0.05$, t-test). During incubation, dead or infertile eggs were removed and counted daily to prevent the spread of fungus. Upon hatching, larvae were removed daily, segregated into two groups ("normal" and dead-and/or-deformed), and counted. Larvae were considered "normal" if obvious deformities were not observed when examined under 30× magnification. Larvae excluded from the "normal" category were those with deformities ranging from curvatures of the spine to gross distortions with various degrees of pericardial edema, smaller premature individuals with reflexed head positions and only primordial eye pigmentation (Kokurewicz 1969), and dead larvae.

Incubation results are normalized percentage values to account for the variations in sample size and percentage viability of eggs from different pairs of adult fish. Data were normalized by setting the maximum success of hatching for any replicate as 100% and all lesser degrees of success within the replicate as a percentage of that maximum. The percentage "normal" hatch data (Table 1) were converted to the arcsin $\sqrt{\text{percentage}}$ transform before statistical analysis. Analysis of variance with unequal sample size was used with Scheffe's test to account for the 12°C exposures added in 1969. Only data for "normal" larvae were analyzed, as the lead and deformed were not deemed a valid contribution to hatching success (Volodin 1960; Kokurewicz 1969).

Larval Growth and Mortality

Rates of growth (wet weight), death, and net biomass gain (wet weight) were determined for groups of larvae reared at temperatures from 10.0 to 29.7°C (Table 2). Larvae for the main portion of the study were from a stock of embryos all incubated at 15°C. Additional lots of larvae from embryos incubated at

TABLE 1. Percentage hatch of "normal" larvae from white sucker (*Catostomus commersoni*) embryos incubated at constant temperatures.[a]

	Nominal temp (means of 1968–69) (°C)						
	6.2	9.0	11.7	15.2	17.2	20.8	24.1
				1968 Test temp and results			
Mean temp (°C)[b]	6.3	9.0		15.3	16.9	20.5	24.0
range	(4.3–7.8)	(8.6–9.7)		(14.9–15.6)	(11.8–17.9)	(20.2–20.8)	(23.9–24.1)
"Normal" hatch (%) replicates							
A	0.0	60.9	—	88.0	75.6	78.1	0.0
B	0.6	66.9	—	87.4	54.1	44.1	0.0
C	1.0	72.2	—	84.5	73.2	63.4	0.0
				1969 Test temp and results			
Mean temp (°C)[b]	6.1	9.0	11.7	15.1	17.6	21.1	24.2
range	(5.9–6.9)	(8.7–10.1)	(10.9–11.9)	(14.9–15.3)	(17.4–17.9)	(20.9–21.2)	(23.9–24.2)
"Normal" hatch (%) replicates							
D	0.0	71.1	71.4	71.0	68.8	27.6	0.0
E	0.8	35.9	54.9	66.4	47.7	39.1	0.0
"Normal" hatch (%) (means of 1968–69)	0.5	61.3	63.2	79.5	63.9	50.5	0.0

[a]Raw data, before normalization and transformation to arcsin $\sqrt{\text{percentage}}$ for statistical tests.

[b]The 95% C.L. of each year's reported mean temperatures was ≤ 0.1°C in all cases except 1968, which was 0.6°C for 16.9°C. Confidence limits < 0.1°C are not reported because thermometer readings were no better than 0.1°C.

TABLE 2. Mean instantaneous rates (percent per day) of growth, death, and net biomass gain of young white-suckers at constant temperatures for the first 4 wk after hatching. The values reported are grand means of successive weekly sampling intervals.[a]

Temp (mean, 95% C.L. and range)	Growth (wet wt)	Death	Net biomass gain (wet wt)
10.0±0.08[b] (9.7–11.3)	0.9 [c]	1.3 [c]	−0.4 [c]
15.7±0.02 (15.1–16.0)	7.4	0.2	7.2
17.9±0.03 (17.6–18.3)	9.7	0.2	9.5
20.8±0.02 (20.5–21.2)	12.0	0.1	11.8
23.9±0.03 (23.7–24.1)	13.2	0.3	13.0
26.9±0.16 (9.0–27.4)	14.8	0.3	14.5
29.7±0.11[b] (28.7–30.5)	9.2	8.3	0.9

[a]Four replicates are represented by the means reported at 15.7, 17.9, and 20.8°C. All other represent two replicates.

[b]Values reported for 10.0°C are for a 5-wk exposure period and for 29.7°C, a 3-wk period.

[c]Vertical lines equally offset to the right of the columns join data points not found statistically different ($P > 0.05$).

9.0, 15.2, and 17.2°C were also reared at 9.0, 15.7, and 17.9°C to compare subsequent growth between fish reared at the same temperature but with different previous thermal experiences (Blaxter 1956). Paired *t*-tests failed to detect any differences due to these pre-test thermal experiences ($P > 0.05$).

Eighty newly hatched larvae were counted and placed in each test unit (10 × 10 × 40.5 cm long) of the temperature-control apparatus. Feeding was ad libitum with live newly hatched brine shrimp which remain, when not eaten, alive and available for hours within the test chambers. Brine shrimp were added in early morning, late afternoon, and whenever during the day it was noticed that most of the food had been consumed. On weekends food was introduced less frequently, only once or twice per day, but the quantity per feeding was greater. The day–night photoperiod was adjusted periodically to equal seasonal photoperiods at Duluth, Minnesota. Rearing units were cleaned daily, and dead fish were counted and removed. At weekly intervals subsamples of 10 fish per test lot were withdrawn and preserved in formalin–picric–trichloracetic solution (Davenport 1960) for later weight determinations. Sample fish were removed after overnight fasting and held an additional 6 h without food before being preserved. Weights of intact preserved fish were determined to the nearest 0.1 mg after blotting to dryness on paper toweling. Daily rates of growth, death, and net biomass gain were calculated after Ricker (1958).

Treatment effects tested were the grand mean rates of growth, death, and net biomass gain at all sampling

intervals: five weekly samples at 10°C, four at each temperature treatment from 15.7 to 26.9°C, and three at 29.7°C. The longer exposure at 10.0°C allowed these slower growing fish to reach a stage of development more nearly comparable to that attained in a shorter time by fish exposed to warmer water. Only a 3-wk exposure at 29.7°C was possible because too few fish survived at 4 wk. The exceptionally variable data for the obviously unfavourable 29.7°C treatment was excluded from analysis (to enable statistical detection of finer differences between other treatments).

Larval TL50 Temperatures

One-, 2-, and 7-day TL50 values were determined for newly hatched and swim-up larvae acclimated to 9–10, 15–16, and 21°C. The TL50s for newly hatched larvae were determined on larvae less than 24 h old, and on swim-up larvae when 50% of the population were capable of sustained swimming. The mean weight per fish was 4–5 mg when newly hatched and 5–7 mg at swim-up.

Larvae were tested in 4 × 4-cm stainless steel screen-walled chambers with shallow (0.5 cm deep) glass-cup bottoms placed in test units of the temperature-control apparatus. Fish were transferred without tempering from acclimation to test temperatures. Feeding was begun after swim-up stage. Deaths were recorded, and dead fish and unused food removed daily.

The TL50 temperatures, 95% confidence limits, and slope function of the line were determined by the method of Litchfield and Wilcoxon (1949). Each time–temperature value was determined with two replicates of 10 fish each.

Results

Embryo Survival

Maximum hatch of "normal" larvae occurred at 15.2°C (79.5% success) (Table 1). Hatching success did not fall significantly below this maximum until temperatures cooler than 9.0 or warmer than 17.2°C were experienced ($P>0.05$). Hatching took place at all test temperatures, but the number of dead and/or deformed larvae increased progressively at temperatures below and above 15.2°C. This was most evident at 6.2°C, where 99% of the larvae produced were deformed, and at 24.1°C, where all of the few larvae that did hatch were deformed.

Larval Growth and Mortality

Daily rates of growth at temperatures from 10.0 to 26.9°C increased with each higher temperature from 0.97 to 14.8%/day and then diminished abruptly at 29.7°C to 9.2%/day (Table 2, Fig. 1B). The highest absolute growth rate was at 26.9°C (14.8%/day). At 20.8°C the growth rate, 12.0%/day, was just statistically less than the maximum ($P<0.05$). At 17.9 and 29.7°C growth was clearly below maximum, 9.7 and 9.2%/day, respectively.

Daily rates of death were uniformly low at temperatures from 15.7 to 26.9°C, ranging from 0.1 to 0.3%/day ($P>0.05$). At 10.0°C the rate increased significantly to 1.3%/day, and at the other extreme, 29.7°C, to 8.3%/day ($P<0.05$).

Daily rates of net biomass gain were high at 23.9 and 26.9°C, 13.0 and 14.5%/day, respectively. At 17.9°C and lower, and at 29.7°C, net biomass gain was markedly reduced from maximum. The negative rate of net biomass gain at 10°C (−0.4%/day) reflected the influence of a death rate coupled with low growth rate which removed weight from the sample population faster than the combined weight gained by survivors.

Larval TL50 Temperatures

Upper TL50 temperatures were approximately the same for newly hatched and swim-up larvae.

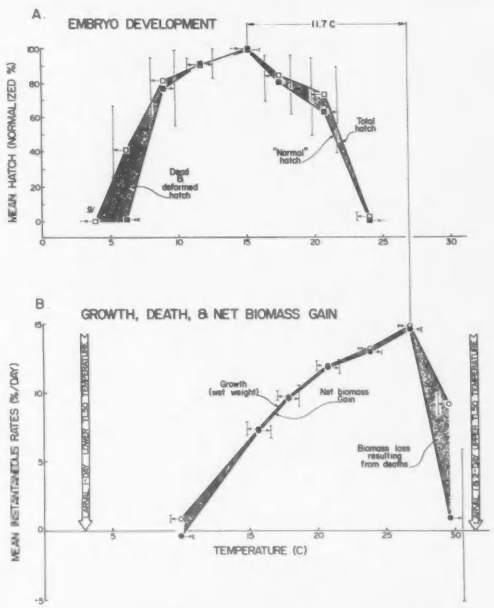

FIG. 1. A, Constant temperature effects on success of white sucker (*Catostomus commersoni*) embryo development; B, instantaneous rates of growth, death, net biomass gain, and upper and lower TL50s of larvae. Vertical bars, set off to the side of the data points, indicate the ranges of replicate means. Point [a] was derived from an ancillary study not described in this report.

TABLE 3. Thermal tolerance limits of white sucker larvae.

Developmental stage at start	Acclimation temp (°C)	Duration of test	TL50 temp (°C)	C.L. (95%)	Slope function
		Lower lethal temp			
Newly hatched	21.2	1-day	<2.9	—	—
		2-day	3.2	3.0–3.4	0.91
		7-day	4.8	4.2–5.3	0.83
Swim-up larvae	21.1	1-day	3.1	2.9–3.3	0.90
		2-day	3.6	b	0.94
		7-day	6.1	5.6–6.6	0.86
		Upper lethal temp			
Newly hatched	21.1	1-day	31.5	30.3–33.0	1.05
		2-day	31.0	b	1.01
		7-day	(28.2)[a]	27.7–28.7	1.08
	15.2	1-day	31.1	b	1.01
		2-day	31.0	30.2–31.8	1.02
		7-day	30.0	29.1–30.9	1.03
	8.9	1-day	29.0	b	1.02
		2-day	29.0	b	1.03
		7-day	28.6	b	1.03
Swim-up larvae	21.1	1- and 2-day	32.0	31.1–33.0	1.03
		7-day	30.5	b	1.02
	15.8	1-, 2-, and 7-day	30.7	b	1.02
	10.0	1- and 2-day	28.5	b	1.01
		7-day	28.1	27.3–28.9	1.03

[a]Questioned by authors; seems inconsistently low.
[b]Insufficient mid-range data to calculate C.L.

When acclimation was at 15–16°C and higher, the 1-, 2-, and 7-day upper TL50 values for both stages were between 30.0 and 32.0°C (Table 3). (An unexplained exception of 28.2°C for newly hatched larvae acclimated to 21°C seemed aberrantly low.) There was little, if any, increase in the upper thermal tolerance by acclimation to temperatures above 15–16°C. At 9.0–10°C acclimation, the 1-, 2-, and 7-day upper TL50 values were reduced to between 28.0 and 29.0°C, and the 7-day TL50 values tend to be a few tenths of a degree lower than for the shorter exposures.

The two larval stages when acclimated to 21°C showed little difference in lower thermal tolerance. The 1- and 2-day lower TL50 values ranged from less than 2.9, the lowest tested temperature, to 3.6°C. Seven-day lower thermal TL50 values were 4.8°C for newly hatched larvae and 6.1°C for swim-up larvae. The TL50 values of fish acclimated to 15°C and lower were below the minimum tested temperature.

OTHER EFFECTS

Spinal deformities were observed in three successive lots of larvae initially reared at 15°C and subsequently transferred to 30°C for 2 wk. Fish in all three lots experienced high death rates, and 100% spinal deformities among survivors. Deaths subsided when survivors were returned to lower temperatures, but spinal curvatures persisted.

Observations also showed that larval suckers avoid temperatures determined to be unfavorable to sustained growth and survival. In all rearing units where water temperatures were 27°C and lower, swim-up larvae were more concentrated at the water input end of the tanks; however, in a 31.2°C test unit, used for TL50 testing, larvae were found at the cooler discharge end. Avoidance of temperatures in excess of 31.2°C was a chance discovery when greatly contrasting ambient temperatures resulted in a thermal gradient (31.2–31.4°C) from the water input end of a rearing unit to the discharge end. The ability of fishes to detect and respond to temperature differences of this magnitude has previously been reported (Bull 1936).

Discussion

As the thermal-responses of the various life stages of the white sucker investigated in this study are contemplated, a marked parallel becomes apparent between the temperatures at

which each life stage occurs in its natural environment and those at which the particular stage has been found to prosper in the laboratory. The first thermal experience of the new individual begins with the fertilization of the egg, an event that takes place in relation to a number of naturally occurring precursors, among which are lengthening daylight hours, a run into spawning areas (usually tributary streams, or shallows of lakes or streams), and a warming trend as the spring season advances.

Raney and Webster (1942) reported spawning runs of white suckers commence as water temperatures reached and exceeded 7.2°C. Initiation of spawning runs at 7.2°C can be interpreted to indicate that naturally spawned embryos would be expected at or above that temperature, so long as seasonal thermal trends persist. Our data indicate that such spawning temperatures would be near the minimum thermal limits for the success of embryos. Viewed in the evolutionary sense, such would suggest that natural selection may have eliminated those individuals possessing genetic traits leading to spawning at lower temperatures. Maximum incubation success in our study occurred at 15.2°C. Raney (1943) observed peak spawning activity at 17.8°C. Both of these temperatures are similar, and cool enough to allow several degrees of warming during the days of incubation without exceeding the $\geq$20.8 but $<$24.1°C tolerance limit for developing embryos. Net rate of biomass gain during the larvae–juvenile stages was relatively poor at 15.2, while the maximum rate was found at 26.9°C. From these observations the importance of a number of interrelated naturally occurring factors becomes more apparent.

No one temperature is best for all life stages of white sucker. There is an 11.7°C increase in temperature between that resulting in greatest success in hatching of embryos and that resulting in most rapid net gain in larval–juvenile weight. That such a trend would be expected comes from the recognition that spawning is in the spring in shallow water where the time between spawning and juvenile growth would be expected to produce several degrees of temperature rise between the occurrence of the two life stages. A further example of the way the sucker has adapted to the restraints of its environment is seen in the movements of young suckers to warmer shallows of lakes and streams (Reighard 1915; Hunstman 1935) apparently taking advantage of the most nearly optimum of available temperatures. Yet these same individuals can be expected to leave these warmer waters when heating results in temperatures exceeding those for their well-being. Our study showed that avoidance would be expected when young suckers encounter waters of 31.2°C and above. Huntsman (1946) observed thermal kills of young suckers when unseasonal temperatures in a Nova Scotia stream reached 31.4°C.

All of these responses indicate an intricate meshing of the organism and the natural conditions in its native habitat. With such an interdependence, the importance of maintaining seasonal temperature cycles, access to native spawning sites, and access to thermal retreats during periods of excessive temperatures becomes apparent.

Aside from the insights gained in this study as it applies directly to white sucker, another use lies in its potential aid to the fish manager interested in promoting the well-being of other species such as trout coinhabiting natural waters with suckers.

Trout, it would seem, prosper in cold waters not so much because cold water is good for them, but possibly more because they are more capable of coping with the cold than are their competitors (Vincent and Miller 1969; Bowen and Coutant 1971). Thus, temperatures reported as optimum for trout when derived from studies where the trout were studied independent of other species (McCormick et al. 1972; Hokanson et al. 1973b) may promote natural competitors such as suckers by tipping the interspecific competitive advantage in favor of the more warmwater competent species. Consequently, when the well-being of trout is sought in a mixed trout–sucker population, it may be advantageous to manage the habitat for temperatures so as to limit the success of competing indigenous suckers.

Acknowledgments

We thank R. F. Syrett and C. F. Kleiner for their assistance and the Minnesota Department of Natural Resources for their assistance in acquiring the brood stock.

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Specificity of Protection Induced in Coho Salmon (*Oncorhynchus kisutch*) by Heat-Treated Components of Two Pathogenic Vibrios

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A series of in vivo comparisons between two marine vibrios pathogenic to pen-reared salmon demonstrated that each organism possessed protection-inducing, heat-stable components that were unique and others that were cross-protective. In all instances, however, immunization with the components of the homologous bacterium produced the highest degree of protection in juvenile coho salmon (*Oncorhynchus kisutch*) against subsequent live-bacteria challenge. Antigenic competition was not detected when fish were immunized with both bacteria, indicating that a bivalent vaccine would be effective against infection by either vibrio.

Key words: fish disease, vibriosis, immunization, *Oncorhynchus kisutch*

SCHIEWE, M. H., AND H. O. HODGINS. 1977. Specificity of protection induced in coho salmon (*Oncorhynchus kisutch*) by heat-treated components of two pathogenic vibrios. J. Fish. Res. Board Can. 34: 1026–1028.

Une série de comparaisons in vivo entre deux vibrions marins pathogènes pour des saumons élevés en enclos démontrent que chaque organisme possède des composantes provoquant une protection et stables à la chaleur applicables à un seul organisme, et d'autres composantes à protection réciproque. Dans tous les cas, cependant, l'immunisation avec les composantes de la bactérie homologue déclenche le plus haut degré de protection chez des jeunes saumons coho (*Oncorhynchus kisutch*) contre une invasion subséquente de bactéries vivantes. Nous ne détectons pas de concurrence antigénique quand les poissons sont immunisés avec l'une et l'autre bactérie, ce qui indique qu'un vaccin bivalent serait efficace contre l'infection par l'un ou l'autre vibrion.

Received December 13, 1976
Accepted February 17, 1977

Reçu le 13 décembre 1976
Accepté le 17 février 1977

VIBRIOSIS, caused by infection with the marine bacterium *Vibrio anguillarum*, is a major obstacle to the successful pen rearing of Pacific salmon (Novotny 1975; Mahnken 1975). Recently, in the Pacific northwest the aquaculture industry has relied heavily on heat- and Formalin-killed bacterins as a means of prophylaxis. However, two serologically distinct vibrios cause mass mortalities in this region (Harrell et al. 1976); it was not known whether the differences involved antigens that are capable of inducing a protective response in immunized or infected fish. If protective antigens differ between the two pathogenic vibrios, vaccines made from one or the other would predictably not be as effective as a bivalent vaccine incorporating antigens from both. Conversely, if antigenic competition occurs when antigens from two vibrios are combined in a single vaccine, this procedure might not be practical. To examine these questions, a series of in vivo comparisons of the two vibrios were conducted; this note reports the results.

Materials and methods — Bacteria used for the preparation of immunogens and for experimental challenge were *V. anguillarum* strain 775 and Vibrio sp. 1669 strain Dom F_1 kid. These isolates, described by Harrell et al. (1976) and Schiewe (1976), were maintained on 50% seawater *Cytophaga* medium containing 0.4% agar (Anacker and Ordal, 1959).

Test fish were juvenile coho salmon (*Oncorhynchus kisutch*) averaging 12 g; they were from a stock of fish that returns to the Northwest and Alaska Fisheries Center, Seattle, Washington. Before experimentation,

Printed in Canada (J4667)
Imprimé au Canada (J4667)

TABLE 1. LD50 values for coho salmon (*Oncorhynchus kisutch*) immunized with strains 775 and Dom F_1 kid, and controls after homologous and heterologous challenge by subcutaneous injection. Initial bacterial concentrations were 2.9×10^9 organisms/ml for 775 and 4.6×10^8 organisms/ml for Dom F_1 kid.

	LD50	
	Challenged with *V. anguillarum* 775	Challenged with V1669-Dom F_1 kid
Immunized with *V. anguillarum* 775	$10^{-7.8}$	$10^{-5.2}$
Immunized with V1669-Dom F_1 kid	10^{-8}	$10^{-3.4}$
Control (not immunized)	10^{-8}	$10^{-6.5}$

10 fish were test bled and the sera were checked for preimmune agglutinins to strains 775 and Dom F_1 kid. Titers against both bacteria were less than two.

Immunogens were prepared from a single lot of each bacterium, grown for 24 h at 25°C in a broth medium composed of 2% Trypticase® Soy Broth (BBL) supplemented with 1% NaCl. Bacteria were harvested by centrifugation and washed 3 times with isotonic saline (0.85% NaCl). Cells were heat-killed (100°C for 30 min), sonicated (5 times for 30 s at 30% maximum intensity on a Biosonik III, Bronwill Scientific), and suspended to a concentration of 20 mg/ml (wet weight) in isotonic saline with 0.3% phenol added as a preservative.

For immunization, fish were anesthetized with MS-222® (100 mg/ℓ) and injected intraperitoneally with 0.1 ml (2 mg) of the appropriate immunogen. Control fish were injected with 0.1 ml of isotonic saline. In the test designed to assess whether antigenic competition occurred, fish were injected with 0.1 ml of a 1:1 mixture of the immunogens (1 mg of each). In all experiments the fish were injected twice (7 days apart) and challenged 11–18 days after the second injection.

Two forms of bacterial challenge were employed in these experiments. In the LD50 determinations, fish were injected subcutaneously at the posterior base of the dorsal fin with 0.1 ml of the appropriate bacterial dilution. In the remaining tests, the challenge procedure consisted of a bath exposure to the virulent bacteria. Fish were held for 30 min in a 1:33 dilution of a 24-h bacterial culture in 1% NaCl (approximately 10^7 organisms/ml). Temperature of the bath ranged from 14 to 16°C.

The fish were maintained before and after bacterial challenge in fresh water at 15°C. After challenge, mortality was monitored daily for at least 7 days or until deaths ceased for 3 consecutive days. Tissues from representative mortalities from all groups were cultured for bacteria to confirm the cause of death.

Results and discussion — In an initial experiment, LD50 values of strains 775 and Dom F_1 kid were determined for fish that were (i) injected with heat-treated components of 775, (ii) injected with the heat-treated components of Dom F_1 kid, and (iii) injected with isotonic saline. The LD50 values, as calculated by the method of Reed and Muench (1938), are shown in Table 1. These data indicate that the highest level of protection against challenge with Dom F_1 kid was afforded by immunization with the homologous antigen(s) and a lesser amount of protection was attained following injection of the heat-treated components of heterologous 775. Fish injected with the components from either pathogenic vibrio survived the challenge from Dom F_1 kid at a higher rate than did saline-injected controls. In contrast, protection against challenge with 775 was essentially negligible after injection of the heat-treated components from either organism. Apparently the high virulence of this isolate under these experimental conditions precluded even homologous protection.

In a second series of experiments, a bath challenge was employed and a single concentration of bacteria was tested against fish immunized as described above. Results of three separate replicates are shown in Table 2. Using Yates' modification of chi square (Langley 1971), statistical comparisons between the groups of fish challenged with 775 showed that significantly higher survival ($P < 0.001$) was achieved by immunization with the homologous antigen(s) over either the heterologously injected or the control groups. No significant differences ($0.3 > P < 0.5$) could be shown between mortality observed in heterologously injected fish when compared with controls. In the case of challenge with Dom F_1 kid, homologously immunized fish survived at a significantly higher rate than did heterologously injected ($P < 0.01$) or control fish ($P < 0.001$). However, it is interesting to note that here a significantly higher survival ($P < 0.001$) was observed in heterologously injected fish when compared with controls.

The final experiment (Table 3) was conducted to ascertain if antigenic competition could be detected between the protective antigens of the two vibrios. When fish were injected with a mixture of the heat-treated components from both vibrios, significantly ($P < 0.01$) higher survival

TABLE 2. Comparison of mortality between groups of coho salmon injected with 775 bacterin, Dom F_1 kid bacterin, or isotonic saline (control) and challenged with 775 or Dom F_1 kid. Bacterial challenge was a bath exposure to live bacteria and the values represent the combined results of three separate trials (total of 58 fish in each group).

	Mortality (%)		
	Immunized with *V. anguillarum* 775	Immunized with V1669-Dom F_1 kid	Control (nonimmunized)
Challenged with *V. anguillarum* 775	0	29	40
Challenged with V1669-Dom F_1 kid	19	2	57

TABLE 3. Comparison of mortality between coho salmon immunized with bivalent vibrio bacterin and controls following challenge with 775 and Dom F_1 kid (total of 40 fish in each group).

	Mortality (%)	
	Challenged with *V. anguillarum* 775	Challenged with V1669-Dom F_1 kid
Immunized	3	0
Control	44	58

was observed in the immunized fish challenged with either 775 or Dom F_1 kid when compared with controls.

The results of these in vivo tests demonstrate that each organism possesses protective, heat-stable components that are unique and others that are cross protective. However, immunization of fish with the bacterial strain used in subsequent challenge always resulted in the highest level of protection. Since antigenic competition was not detected, these data clearly indicate that control of vibrios would be best accomplished by immunization with a bivalent vaccine combining antigens from both pathogenic vibrios.

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Food of Some Benthic Harpacticoid Copepods

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BROWN, T. J., AND J. R. SIBERT. 1977. Food of some benthic harpacticoid copepods. J. Fish. Res. Board Can. 34: 1028–1031.

Feeding rate of harpacticoid copepods on different food sources was measured using a double isotope technique. Heterotrophically derived carbon was ingested at a rate 9 times faster than autotrophically derived carbon.

Printed in Canada (J4455)
Imprimé au Canada (J4455)

BROWN, T. J., AND J. R. SIBERT. 1977. The food of some benthic harpacticoid copepods. J. Fish. Res. Board Can. 34: 1028–1031.

Nous avons déterminé à l'aide d'une technique à isotope double le taux d'alimentation de copépodes harpacticoïdes avec différentes sources d'aliments. Le carbone de source hétérotrophe est ingéré à un rythme 9 fois plus rapide que le carbone de source autotrophe.

Received July 12, 1976
Accepted March 14, 1977

Reçu le 12 juillet 1976
Accepté le 14 mars 1977

RECENT studies have shown that benthic harpacticoid copepods are important components of the diet of juvenile salmonids during their estuarine life (Kaczynski et al. 1973; Mason 1974; Feller and Kaczynski 1975). Reports in the literature on the diet of harpacticoids are confusing. Some authors (Lear and Oppenheimer 1962; Shiraishi 1966; Inoue and Aoki 1969; Battaglia 1970; Betouhim-El and Kahan 1972) report that harpacticoids can thrive on an algal diet. Others (Seki 1966; Gilat 1967; Gray 1968; Barr 1969; McIntyre 1969; Lasker et al. 1970; Khaylov and Yerokhin 1971) report that bacteria are an additional essential component of their diet. We report some simple experiments designed to determine the relative importance of autotrophic (i.e. algae) and heterotrophic (i.e. bacteria) sources of carbon to some harpacticoid copepods.

Materials and methods — Samples of surface sediments containing natural populations of benthic microorganisms were collected with cores from the Nanaimo River estuary, B.C. (49°10′N, 123°54′W) and separately enriched to encourage the growth of algae or bacteria. The autotrophic enrichment was a mixture of inorganic nutrients, trace metals, and vitamins and was incubated in the light. The heterotrophic enrichment was 1 g glucose/ℓ and was incubated in the dark. Both enrichments received an additional 0.5 g/ℓ of sterilized sand and were incubated for 10 days at 10°C. After incubation, 50 μCi/ℓ $NaH^{14}CO_3$ was added to the autotrophic culture and 50 μCi/ℓ ^{3}H-glucose to the heterotrophic culture. After 12 h of uptake, the cultures were used for the feeding experiments. The activity of the isotope in each culture was determined by liquid scintillation counting using a TEG (479 ml toluene, 479 ml ethylene glycol monoethylether, 42 ml spectrofluor) cocktail. Aliquots (10 and 20 ml) of each culture were filtered on glass fiber filters and the carbon on each filter was determined using a Coleman (Model No. 33) carbon hydrogen analyser. The specific activity (microcuries per micrograms of carbon) of each isotope was then calculated.

Mixed populations of harpacticoids were collected, using a diver-operated plankton net, fished within 10 cm of the sediment surface in the same areas as the microbial populations. Animals were concentrated and separated from the detritus using a disposable pipette, and then held for 24 h before feeding to ensure that their guts were empty. Aliquots of each culture containing known activities were filtered, washed, and presented to a population of approximately 1000 copepods. For each measurement, 50 animals were removed from the experimental vessel, killed with 5% Formalin, measured for length, and cleaned to remove detritus. Activity of each isotope in the copepods was determined by counting with a Nuclear Chicago Isocap 300 liquid scintillation counter after treatment with PCS (Amersham/Searle) solubilizer. The technique of counting samples with dual labels is discussed by Bush (1964). The DPM of each isotope in the sample was calculated according to the manufacturer's instructions. The weight of copepods in each sample was calculated from an empirically determined length–weight relationship (Fig. 1). Amount of carbon taken up from each source was calculated from the DPM's in the copepods and the specific activity of each food.

The length–weight relationship was produced by sorting the copepods into length categories using a dissecting microscope with an ocular micrometer. The copepods were dried at 105°C for 4 h. Animals in each size-class were counted and weighed on a Cahn electrobalance and an average weight per animal was calculated.

Results and discussion — Uptake of carbon from both food sources was approximately linear with time and did not level off during the first 5–7 h (Fig. 2). Animals killed by a brief exposure to 40°C did not show uptake of either isotope

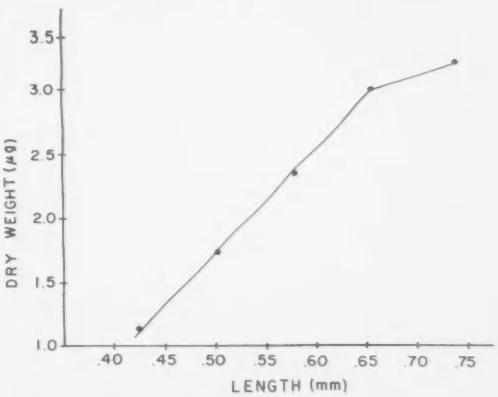

FIG. 1. Length–weight relationship for harpacticoid copepods. Each point represents the average weight per animal in an aggregate sample of approximately 50 animals.

TABLE 1. Summary of feeding experiments.

Numerically dominant harpacticoid species	Assimilation rate μg C/(mg dry wt · h) least squares regression fit		Bacterial C: Algal C	
	Algal C	Bacterial C	Food	Assimilation rate
Harpacticus uniremis and *Tisbe furcata*	0.37	3.3	1.6	8.8
H. spinulosus and *H. uniremis*	0.39	4.1	0.93	10.6
Dactylopodia crassipes	5.1	46.0	0.52	9.0

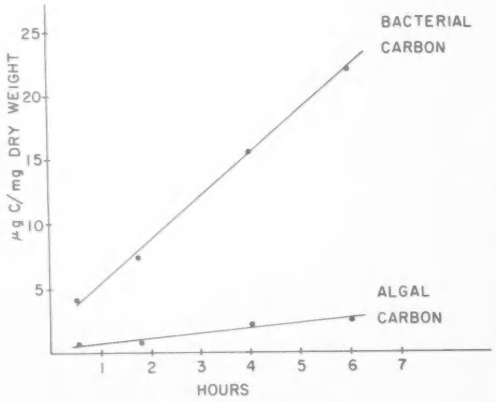

FIG. 2. Uptake of labeled foods by a mixed population of *Tisbe furcata* and *Harpacticus uniremus*. The least squares lines are:

uptake = $0.464 + 0.374 \times$ h for algal C, and

uptake = $2.06 + 3.29 \times$ h for bacterial C.

above background activity. Since the copepods filled their guts several times during the course of the experiment (as evidenced by fecal pellet production) and since the uptake curve remained approximately straight, we are calling the observed uptake assimilation (i.e. ingestion minus defecation). A least squares regression line was fitted to the data and the slope used as an estimate of assimilation rate. Results from three experiments indicate that these harpacticoid copepods assimilate heterotrophic foods at rates roughly 8–10 times greater than they assimilate autotrophic foods (Table 1). The two food sources were presented in similar proportions, so that the difference in assimilation rates is due to differential uptake.

The reasons for the large differences in assimilation rates within and between these harpacticoid species is not known. Scanning electron micrographs suggest that there are differences in size and morphology of mouthparts between *Harpacticus uniremis* and *Dactylopodia crassipes*. Food particle size is known to be an important determinant of feeding rate in other systems (Parsons and LeBrasseur 1970; Frost 1972). Therefore, food size may account for the differences in assimilation rate between food sources and between harpacticoid species. The autotrophic enrichments contained a wide variety of diatoms including some larger (>200 μm) forms such as *Biddulphia* sp. and *Melosira* sp. as well as many small ($\cong$ 20 μm) naviculoids. These organisms were much larger than the bacteria (<5 μm) present in the heterotrophic enrichment. Further experiments are required to test this hypothesis.

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A Hand-Operated Suction Sampler for the Collection of Subtidal Organisms

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TANNER, C., M. W. HAWKES, P. A. LEBEDNIK, AND E. DUFFIELD. 1977. A hand-operated suction sampler for the collection of subtidal organisms. J. Fish. Res. Board Can. 34: 1031–1034.

A hand-operated suction sampler is described for use by SCUBA divers. The sampler is simple in construction and compact in size, and it provides a means by which diminutive benthic algae, invertebrates, or fish may be collected.

Key words: algae, benthic organisms, sampling device, SCUBA, suction sampler

TANNER, C., M. W. HAWKES, P. A. LEBEDNIK, AND E. DUFFIELD. 1977. A hand-operated suction sampler for the collection of subtidal organisms. J. Fish. Res. Board Can. 34: 1031–1034.

Les auteurs décrivent un échantillonneur à succion commandé à la main et pouvant être utilisé par les plongeurs en scaphandre autonome. L'échantillonneur est de construction simple et de taille compacte, et permet de cueillir des algues benthiques, des invertébrés ou des poissons de très petite taille.

Received December 20, 1976
Accepted March 2, 1977

Reçu le 20 décembre 1976
Accepté le 2 mars 1977

THE collection of subtidal coenocytic, filamentous, and diminutive thalloid seaweeds by hand is difficult and time consuming. Numerous suction sampler designs are available, but these are primarily for the collection of infauna on sandy or muddy bottoms (Holme 1971; Mackey 1972; Christie and Allen 1973). The rocky bottom airlift samplers described by Jones (1971) and Hiscock and Hoare (1973) are relatively large and require an external source of air. The more compact hand-operated suction sampler described by Gulliksen and Derås (1975) is a closed pump, and this requires the sample container to be changed after each stroke of the pump. Bleakney (1969) and Smith (1973) described compact samplers that can be pumped continuously, but these are designed in such a way that changing of the sample container in the field is difficult or impossible.

We designed a simple hand-pumped suction sampler to be used by divers, especially for the

Printed in Canada (J4673)
Imprimé au Canada (J4673)

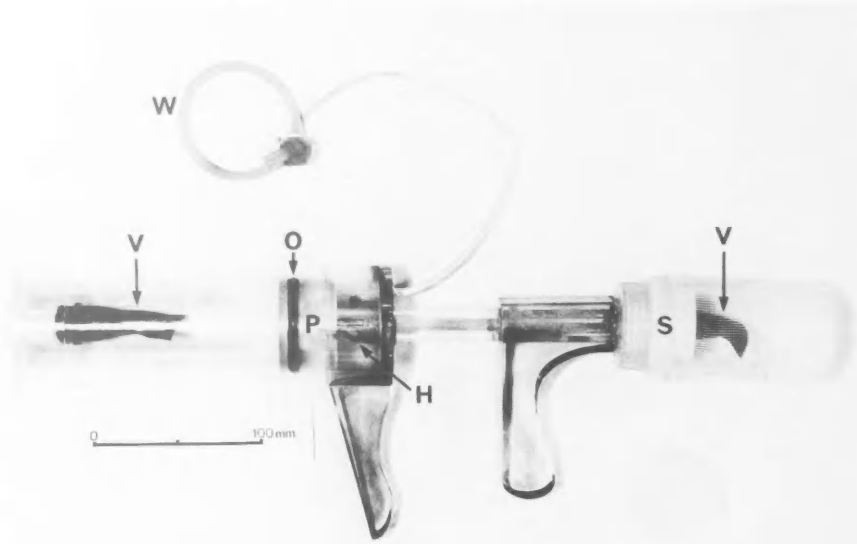

FIG. 1. Suction sampler showing valves (V), piston (P), O-ring (O), hook for attachment of rubber band (H), sample bottle (S), and wristband (W).

collection of small benthic seaweeds. This sampler is compact and has a flow-through design and removable sample containers.

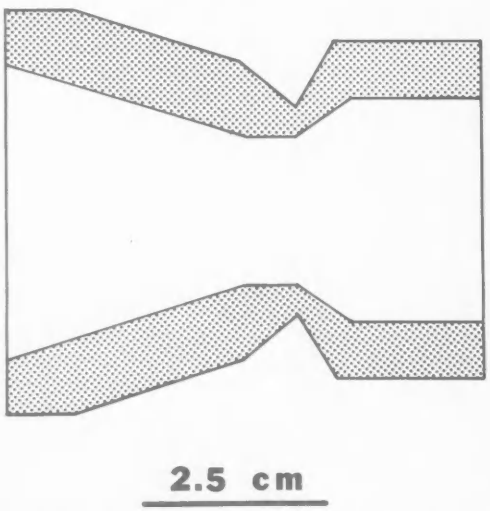

FIG. 2. Pattern for valves to fit 19-mm tubing. The valves are made of two pieces of neoprene glued along two sides (shaded area).

Description and Construction of Sampler — The suction sampler consists of a piston pump with a hollow piston rod serving as an outflow pipe which empties into a sample bottle (Fig. 1). The pump cylinder, outside diam 63.5 mm (2½ in.), the intake and outflow pipes, 19 mm (¾ in.) or 25.4 mm (1 in.), and the end caps, 69.9 mm (2¾ in.), are of plexiglass piping with 3.2-mm (⅛-in.) thick walls. The plexiglass piston is 56 mm diam. A 50.8-mm (2-in.) O-ring fitted into a groove in the piston provides a snug seal with the cylinder. The two end caps fit tightly over the ends of the cylinder, but are removable to enable easy access to the internal parts. The end of the posterior cap has six 9-mm holes that allow water exchange during pumping. Tension on the piston is provided by two rubber bands running through the holes in the posterior cap to two brass hooks screwed into the back of the piston.

The valves are made of 0.5-mm thick neoprene obtained from heavy dish-washing gloves or chemical resistant gloves, and are glued together as shown in Fig. 2 with a neoprene glue (such as Anchor-weld, available from Roberts Consolidated Industries, Inc., Monrovia, California). Valves from double hose SCUBA regulators may also be adapted for use. The valves are attached to the intake and outflow pipes with rubber bands.

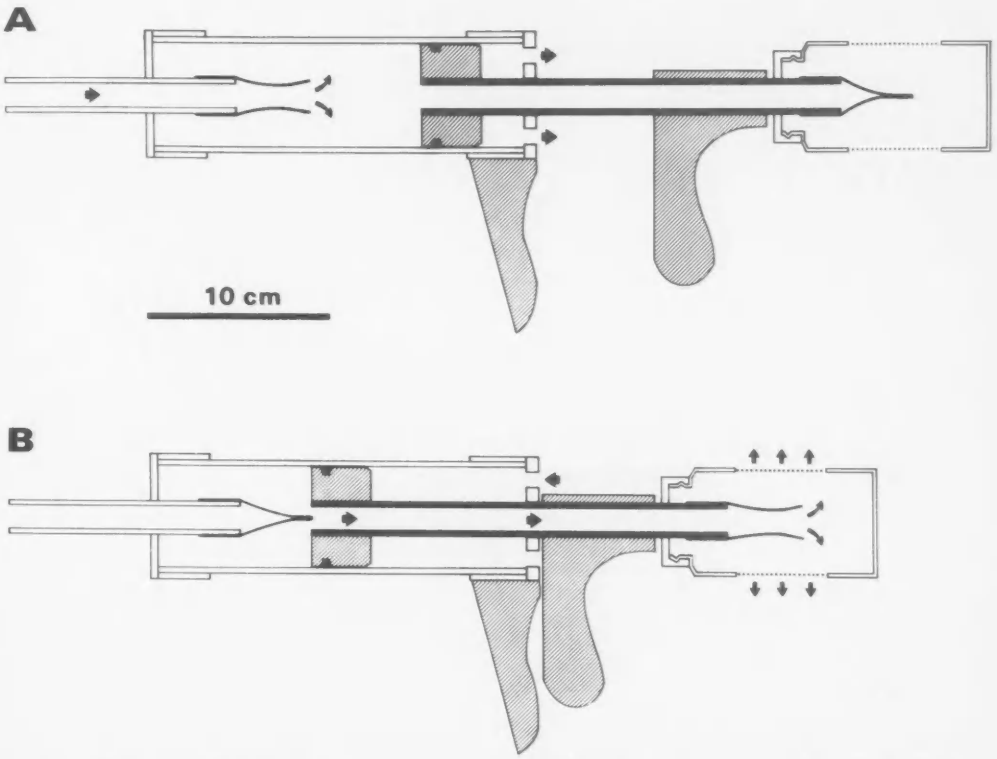

FIG. 3. Longitudinal sectional view of the suction sampler indicating pumping action (arrows indicate water flow), A, As the piston is pulled backwards by rubber bands, decreased pressure in the pump chamber collapses the posterior valve and pulls water and sample into the pump chamber; B, as the piston is pushed forward by squeezing the handles together, increased pressure in the pump chamber collapses the anterior valve and pushes water and sample into the sample bottle.

Sample bottles are made from 250- or 500-ml wide-mouth Nalgene polyethylene jars that have panels cut out of their sides or end and replaced with 1-mm mesh netting. For some uses clear plastic bottles may be preferable. For the collection of algae the bottle is attached to the sampler by a lid mounted on the outflow pipe and may be removed and sealed by another lid attached to the bottle by string. If it is preferable not to open the jar underwater, as is the case when collecting active invertebrates or fish, a valve may be mounted on the inside of each jar which is then connected to the sampler with 12.7-mm (½-in.) male and female screw-mount polyvinyl chloride pipe connectors.

Discussion — The backward and forward movement of the piston alternately sucks the sample into the pump chamber (Fig. 3A) and pushes the sample through the outflow pipe into the sample bottle (Fig. 3B). The advantages of this sampler are: (1) it can easily be held and operated by one hand, leaving the other hand free to remove organisms from the substrate, (2) the amount of sample collected is not limited to a single stroke of the pump, (3) it is not dependent on a compressed air source for operation, and (4) the sample containers may be removed and replaced underwater.

The sampler was found to be extremely useful for collecting coenocytic, filamentous, and foliose algae, e.g. "*Halicystis ovalis*," *Derbesia marina*, *Antithamnion defectum*, *Syringoderma abyssicola*, and *Dictyota binghamiae*. Our use of the sampler was strictly qualitative; however, it could be used to clear small quadrats, e.g. ⅛ m^2, after all large organisms have been removed and would give a quantitative sample down to the 1-mm size range. By employing a smaller mesh size on the sample

bottle, quantitative samples below 1 mm could be made. Experimentation with the sampler has demonstrated its usefulness for the collection of small crustaceans, nudibranchs, and slow-moving fish.

Acknowledgments — The authors thank Mr K. Jeffries for his help in construction of the sampler. National Research Council of Canada Grant A-4471 to Dr R. F. Scagel provided for construction of the sampler and financial support to P. A. Lebednik. M. Hawkes and C. Tanner were supported by National Research Council Postgraduate scholarships.

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Effect of Shock Exposures of Chlorine on the Plasma Electrolyte Concentrations of Adult Rainbow Trout (*Salmo gairdneri*)

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Blood was pooled from randomly selected 3-yr-old rainbow trout (*Salmo gairdneri*) before addition of chlorine to their water environment and afterward when fish began to gulp for air and lose equilibrium. In five duplicate tests, plasma concentrations of phosphorus, magnesium, iron, copper, zinc, and potassium increased substantially in the stressed fish. Calcium concentration was also higher, but not significantly so in the plasma of the test fish as compared with those of the controls. Sodium was the only electrolyte that dropped substantially ($P < 0.01$) in the test fish as compared with the controls.

Chlorine toxicity appeared to disturb the mineral homeostasis in the fish blood. Rapid recruitment of electrolytes from the environment and movement into the plasma, a strong mineral retention mechanism, or mobilization of body mineral stores worked together or individually to compensate for those minerals lost with water during hemoconcentration.

Key words: rainbow trout, plasma electrolytes, chlorine, hemolysis, hematology, toxicology

ZEITOUN, I. H., L. D. HUGHES, AND D. E. ULLREY. 1977. Effect of shock exposures of chlorine on the plasma electrolyte concentrations of adult rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 34: 1034–1039.

Des échantillons de sang prélevés sur des truites arc-en-ciel (*Salmo gairdneri*) de 3 ans choisies au hasard ont été mis en commun avant l'addition de chlore à l'eau de leur milieu et après quand les poissons commencent à avaler de l'air et à perdre l'équilibre. Au cours de cinq essais en double, les teneurs dans le plasma en phosphore, magnésium, fer, cuivre, zinc et potassium

Printed in Canada (J4658)
Imprimé au Canada (J4658)

augmentent substantiellement chez les poissons soumis au stress. La teneur en calcium est également plus élevée, mais non de façon significative dans le plasma des poissons d'essai comparativement à celle des témoins. Le sodium est le seul électrolyte qui diminue de façon marquée ($P < 0.01$) chez les poissons d'essais comparativement aux témoins.

La toxicité du chlore semble déranger l'homéostasie minérale dans le sang des poissons. Le recrutement rapide d'électrolytes de l'environnement et passage dans le plasma, un mécanisme fort de rétention des minéraux, ou la mobilisation des minéraux entreposés dans les tissus agissent conjointement ou individuellement pour compenser les minéraux perdus en même temps que l'eau durant l'hémoconcentration.

Received December 6, 1976
Accepted March 4, 1977

Reçu 6 décembre 1976
Accepté le 4 mars 1977

THERE is considerable concern regarding the potential effects on aquatic life of the widespread use of chlorine as a defouling agent in power plant cooling systems and as a disinfectant of wastewaters. Current effluent regulations promulgated by the U.S. Environmental Protection Agency limit the discharge of free available chlorine from power plants to a maximum concentration of 0.5 mg/ℓ and an average of 0.2 mg/ℓ for not more than 2 h daily (U.S. EPA 1974). However, Basch and Truchan (1974) recommended a total residual chlorine concentration not exceeding 0.04 mg/ℓ when water temperature is below 21.1°C (70°F) and 0.2 mg/ℓ when water temperature is above the 21.1°C as safe for all fish species. That chlorine may have toxic effects on fish species of sport and commercial interest is obvious as a consequence of an increasing number of research reports and reviews (Brungs 1973; Brooks and Seegert 1975). Most reports deal with mortality and toxic limits and little attention has been focused on the mode of chlorine's action and its effect on fish physiology.

The biocide role of chlorine is believed to result from its interference with normal cell function. Chlorine disrupts an enzyme system, probably triose phosphate dehydrogenase, essential for the utilization of glucose (Green and Stumpf 1946). Recently, Grothe and Eaton (1975) concluded that chlorine toxicity to fish was mainly a consequence of the oxidation of hemoglobin to methemoglobin, which in turn reduces the oxygen-carrying capacity of the blood and hence disrupts metabolism. However, Buckley et al. (1976), who studied the effects of chlorinated wastewater on coho salmon (*Oncorhynchus kisutch*), concluded that the resulting methemoglobenemia was not biologically significant. In the meantime, Zeitoun (1977) found that methemoglobenemia, in association with hemolytic anemia due to acute chlorine toxicity, produced signs of hypoxia. This hypoxia was associated with hemoconcentration, which Swift and Lloyd (1974) have proposed is a result of increased renal output. Hunn (1969) reported that hypoxia, and the associated increase in urine flow, resulted in increased urinary loss of sodium, potassium, and magnesium.

The following was undertaken to document the changes in the concentrations of various plasma electrolytes as a consequence of acute chlorine toxicity and the resultant hemoconcentration.

Materials and methods — Five separate tests were conducted on replicate groups of 3-yr-old rainbow trout (*Salmo gairdneri*). Approximately 15 fish were used in each replicate. These fish were purchased from a registered fish farmer in the Grand Haven area, Michigan. Each group of fish was maintained in a 450-ℓ tank receiving its water from one of the Consumers Power Company intake channels. This water was a blend of water from Lake Michigan and Pigeon Lake. Pigeon Lake is adjacent to and flows directly into Lake Michigan. However, since the amount of cooling water required by the plant is higher than that supplied by Pigeon Lake, the flow is reversed so that Lake Michigan water flows into Pigeon Lake where the plant intake and test site are located. Water was circulated through the test tanks at the rate of 7.5 ℓ/min after being heated and aerated.

Fish were acclimated to the tanks' environment for at least 6 days, during which they were fed once daily with commercial Master Mix Fish Grower Pellets (36% minimum crude protein: Central Soya and Subsidiaries, Fort Wayne, Indiana). Feeding was halted 18 h before the test. The average weights and total lengths (TL) of the fish used in each test (with two replicates, A and B) were as follows:

Test no.	No. of fish	TL ± SE (mm)	Wt ± SE (g)
1			
A	13	251.6± 7.4	209.4±20.7
B	13	257.3± 7.9	218.2±19.4
2			
A	11	280.8± 6.0	317.1±20.8
B	15	281.2± 6.8	325.0±27.8
3			
A	13	274.6± 4.4	312.1±13.6
B	16	278.6± 6.9	326.2±21.2
4			
A	15	261.8± 7.9	186.4±22.1
B	10	278.5±10.6	208.4±31.0
5			
A	18	258.8± 7.0	185.6±15.7
B	11	282.5± 7.0	231.2±17.5

Prior to chlorination, individual fish were randomly removed from the tank and dried thoroughly. Blood

TABLE 1. Total and free residual chlorine (mean ± SE) and quality of water used in the five tests (means); DO_2 = dissolved oxygen; DS = dissolved solids. Total alkalinity and hardness measured as $CaCO_3$.

	Test 1	Test 2	Test 3	Test 4	Test 5
Total residual Cl (mg/ℓ)	3.86±0.08	2.47±0.23	2.75±0.31	1.67±0.096	3.50±0.16
Free residual Cl (mg/ℓ)	3.10±0.08	1.16±0.32	1.39±0.35	0.29±0.019	2.35±0.30
Temp (°C)	10.8	11.0	12.5	13.5	14.6
DO_2 (mg/ℓ)	9.8	9.5	9.2	6.91	8.94
pH	7.9	7.8	7.9	7.64	8.01
Total DS (mg/ℓ)	850	276	292	—	235
Total alkalinity (mg/ℓ)	129	94	90	90	100
Hardness (mg/ℓ)	172	150	168	127	140
Total chlorides (mg/ℓ)	14.0	18.2	17.2	11.3	9.26
Metals					
Ca (mg/ℓ)	37.4	35.1	34.7	34.3	34.0
P (mg/ℓ)	0.8	0.3	0.3	0.4	0.3
Mg (mg/ℓ)	11.6	9.2	8.9	7.6	10.5
Na (mg/ℓ)	11.4	9.9	9.3	4.4	4.6
K (mg/ℓ)	0.8	1.3	1.3	0.7	0.4
Fe (mg/ℓ)	1.2	1.0	1.3	0.7	0.9
Cu (μg/ℓ)	4.0	0.4	0.4	1.8	1.3
Zn (μg/ℓ)	—	90	90	81	—

was collected (by severing the caudal peduncle) in tubes treated with ammonium heparin. Normally, blood from three to five control fish was pooled to obtain the 14 ml of blood required for the analysis. The remaining fish in each tank were then exposed to chlorine by the addition of 16% sodium hypochlorite solution after the water circulation system was closed. Total residual chlorine (measured amperometrically), temperature, dissolved oxygen, and pH were determined every 5–7 min (Table 1).

Blood collection from each group of fish exposed to chlorine began when fish started to gulp for air and to lose their equilibrium. The levels of chlorine varied (in part because of differences in water quality) with each test (Table 1), and these variations seemed to be unimportant, since chlorine toxicity is a function of concentration and exposure time, and fish were not removed until signs of hypoxia were evident. Procedures of blood sampling and handling were similar to those described for the controls, except 7–10 fish were used to get adequate plasma because of the hemoconcentration. Hematocrit values were determined using the microhematocrit method described by McGovern et al. (1955). The heparanized fish blood was centrifuged and plasma was withdrawn, placed in small vials, and stored at −4°C until analyzed. Calcium, magnesium, iron, copper, and zinc were determined by atomic absorption, sodium and potassium by atomic emission, and phosphorus by visible light spectrophotometry using the Gomori (1942) method.

Data were tested for significance using the Student's *t*-test.

Results and discussion — Plasma mineral analysis of rainbow trout (Table 2) showed that pronounced changes occurred due to chlorine toxicity. All mineral concentrations except calcium and sodium rose significantly above controls. The increase in plasma iron concentration was small and fell short of statistical significance ($P = 0.062$) despite distinguishable hemolysis in the plasma of stressed fish. Blood hemolysis has been reported for fish exposed to sublethal (Buckley et al. 1976) and lethal levels of chlorine (Zeitoun 1977). The amount of iron released from the stressed rainbow trout erythrocytes to the plasma due to their fragility and rupture could be used to establish the severity of the hemolytic anemia. The exposure of red blood cells to oxidants such as chlorine results in the formation of peroxides (Cohen and Hochstein 1964). These peroxides are responsible for erythrocyte fragility and hence the release of hemoglobin and the iron that hemoglobin contains. Assays for the hemoglobin in fish plasma were previously employed as indicators of the degree of hemolytic anemia (Zeitoun 1977). In this study, plasma iron was used instead, and the degree of hemolysis was expressed as the percentage increase of plasma iron concentrations in chlorine-exposed fish above the controls. The percentage increase was 1313, 393, and 184% for the first, four and fifth tests, respectively (Table 2).

The substantial increase in the concentration of the majority of plasma minerals due to chlorine exposure seemed directly related to the increase in blood viscosity, which was easily distinguishable during blood collection. This hemoconcentration was confirmed for fish suffering from acute chlorine stress (Zeitoun 1977) and hypoxic stress

TABLE 2. Concentrations of various plasma electrolytes of control and chlorine-stressed rainbow trout (*Salmo gairdneri*)

	Test number							
	1	2	3	4	5	Mean	Difference (±SE)	*P*
Cu (μg/100 ml)								
Control	114.8	126.7	158.4	110.9	115.9	125.2	44.7	<0.01
Test	142.2	213.0	196.4	172.2	147.2	169.9	(10.97)	
Zn (μg/100 ml)								
Control	1611.0	2425.1	2224.4	1322.4	1581.0	1832.8	866.1	<0.02
Test	1758.8	3100.8	2554.6	3400.7	2679.8	2699.0	(296.21)	
Fe (μg/100 ml)								
Control	136.8	—	—	150.0	141.5	142.7	739.6	0.062
Test	1796.2	—	—	590.0	260.6	882.4	(308.02)	
Na (mg/100 ml)								
Control	349.6	349.6	350.4	334.8	325.4	342.0	−49.7	<0.01
Test	293.7	292.8	305.0	299.8	270.0	292.3	(5.03)	
K (mg/100 ml)								
Control	9.0	2.6	3.6	1.9	3.2	4.1	2.1	<0.03
Test	11.4	6.9	4.0	2.6	6.2	6.2	(0.77)	
Ca (mg/100 ml)								
Control	30.8	—	—	23.6	22.4	25.6	4.2	0.13
Test	30.8	—	—	32.2	26.5	29.8	(2.32)	
P (mg/100 ml)								
Control	19.3	—	—	15.5	13.8	16.2	3.0	<0.01
Test	20.6	—	—	18.8	18.4	19.2	(0.70)	
Mg (mg/100 ml)								
Control	4.0	4.9	4.8	3.5	3.4	4.1	0.8	<0.01
Test	4.2	5.9	6.0	4.8	3.8	5.0	(0.17)	
Exposure time (min)	8	19	20	56	17			

TABLE 3. Anticipated changes of the concentration of plasma minerals of rainbow trout as a result of an average increase of 32% of hematocrit values of fish blood after chlorine exposure. Average hematocrits for individual control groups were 43, 48, 51, 42, and 42%, while those for fish exposed to chlorine were 62, 65, 60, 56, and 53%.

	Anticipated values	Measured values	Difference	Difference (%)
Cu (μg/100 ml)	165.3	169.9	4.64	2.7
Zn (μg/100 ml)	2419.3	2699.0	279.7	10.4
Fe (μg/100 ml)	188.4	882.4	694.0	78.7
Na (mg/100 ml)	451.4	292.3	−159.1	−54.4
K (mg/100 ml)	5.4	6.2	0.79	12.7
Ca (mg/100 ml)	33.8	29.8	−4.0	−13.4
P (mg/100 ml)	21.4	19.2	−2.2	−11.4
Mg (mg/100 ml)	5.4	5.0	−0.41	−8.2

(Swift and Lloyd 1974). Calcium concentration of the stressed fish plasma was higher than that of controls in the fourth and fifth tests (Table 2), while the first test produced no difference between treatments. As a consequence of excluding the first test data from the statistical analysis, the differences between treatments in the last two tests were substantially different ($P < 0.05$). However, using the calculated averages for all tests, plasma calcium was slightly but not statistically higher ($P = 0.13$) in the test group as compared with the controls.

A rise in hematocrit values of rainbow trout lethally stressed with chlorine was observed in

these tests. The calculated percentage increase was approximately 32% above controls (Table 3). By using this value and assuming that this increase was due only to blood dehydration, it was evident that the concentratoins of some electrolytes, such as Na, Ca, P, and Mg, were less than anticipated. Therefore, these minerals seemed to be either excreted in the urine (Hunn 1969) or through the gills (Randall et al. 1972). Abnormally high excretion of various minerals, including K, Na, and Mg, following hypoxic stress has been associated with diuresis (Hunn 1969). Swift and Lloyd (1974) also found that hemoconcentration is a result of diuresis. A loss of minerals via urine seems likely, but Randall et al. (1972) reported that stress caused a great loss of sodium across the gills due possibly to a rise in the levels of circulating catecholamines and an alteration in blood flow through the gills. The water diuresis and salt secretions were also suggested by Holmes (1959) to be influenced by hormones.

The calculated iron concentration in stressed fish was prominently less than that measured. This was definitely related to the hemolysis, which released erythrocyte iron into the plasma.

General discussion — Chlorine-induced stress, associated with hemoconcentration, demonstrably disrupted plasma electrolyte balance, which by itself is considered an important factor in the upset of general metabolic functions of fish. Kirk (1974) concluded that electrolyte imbalance makes fish less tolerant to any further stress. Also, stressed fish are unable to provide sufficient energy to maintain blood mineral homeostasis in spite of the immediate mobilization of carbohydrate stores following hypoxic stress (Heath and Pritchard 1965).

Our data suggest that fish possess an active mechanism(s) to compensate for the losses of Cu, Zn, Fe, K, Na, Ca, P, and Mg. The compensation for each mineral might not be the same as the unequal amounts of their losses. An increased influx of ions through the gills (Randall et al. 1972) or mobilization of these ions from body stores (Stanley and Colby 1971) is a possible mean. Addition of NaCl to the water was reported to enhance the survival of stressed fish (Collins and Husley 1963). Accordingly, the rate at which stressed fish are able to compensate for losses of water and ions seems to determine the severity of the stress.

In conclusion, the changes in the plasma mineral concentrations that were associated with acute chlorine poisoning could be used by fisheries biologists to diagnose, or at least narrow the diagnosis of, the chlorine toxicity effect. Although some of these observations could be similar to those made with hypoxic stress, hemolysis is specific to oxidants such as chlorine and could be considered in association with hemoconcentration as a symptom of chlorine toxicity.

Acknowledgments — The assistance of Dr W. G. Bergen and Ms M. Shaft is appreciated. We thank Dr J. Z. Reynolds, Dr E. R. Miller, and Dr J. J. Rochow for reviewing the manuscript; C. Snow, R. Zimmerman, and M. Lively for the collection of the blood samples; and Mrs J. G. Peck for her secretarial help.

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Establishment of White Perch, *Morone americana*, in Lake Erie[1]

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White perch, *Morone americana*, was first reported in Lake Erie in 1953. No further reports of capture were recorded until 1973, when one fish was taken. Three other captures were confirmed in 1974, and 34 in 1975. All but 3 of the 38 specimens were taken in the warm, shallow western basin and the extreme eastern end of the central basin. The widespread distribution and the sizable numbers of specimens collected in 1975 strongly indicate that this nonendemic species has become established in Lake Erie.

Key words: white perch, range, Lake Erie

BUSCH, W.-D. N., D. H. DAVIES, AND S. J. NEPSZY. 1977. Establishment of white perch, *Morone americana*, in Lake Erie. J. Fish. Res. Board Can. 34: 1039–1041.

Le bar-perche, *Morone americana*, a été signalé pour la première fois dans le lac Erié en 1953. Il n'y eut pas d'autres mentions de capture jusqu'en 1973, alors qu'un individu fut capturé. Trois autres captures furent confirmées en 1974 et 34 en 1975. Les 38 individus, sauf 3, ont été capturés dans le bassin occidental chaud et peu profond, et à l'extrémité orientale du bassin central. La distribution étendue et le nombre appréciable de spécimens recueillis en 1975 indiquent fortement que cette espèce non endémique s'est établie dans le lac Erié.

Received January 5, 1977
Accepted March 19, 1977

Reçu le 5 janvier 1977
Accepté le 19 mars 1977

UNTIL recently, the white perch, *Morone americana*, has been conspicuously absent in commercial fish landings from Lake Erie after the collection of the first specimen more than 20 yr ago. Larsen (1954) reported the capture of a white perch early in the summer of 1953 by a commercial pound net fisherman near Erie, Pennsylvania (Fig. 1), and two others were reported later that year from Ohio waters near Conneaut and Fairport (Trautman 1957). Further occurrences of white perch in Lake Erie were not reported until March 1973, when a 5-yr-old male was caught off Port Clinton, Ohio, by a commercial fisherman. Three others (a 2-yr-old female and 5- and 2-yr-old males) were confirmed in 1974, all from Ohio waters of the western basin.

[1]Contribution No. 526, Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Mich. 48105, USA.

Printed in Canada (J4684)
Imprimé au Canada (J4684)

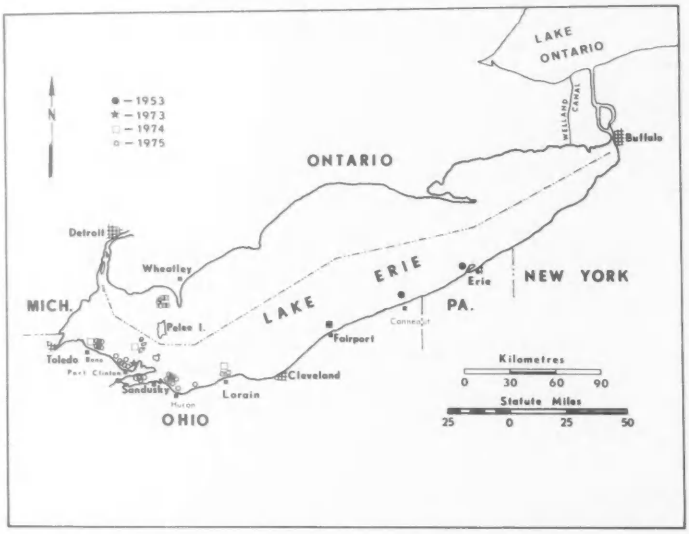

FIG. 1. Locations of reported captures of white perch (*Morone americana*) from Lake Erie in 1953 and 1973–75.

These observations led us to believe that the white perch had indeed become established in Lake Erie.

Extension of the white perch's range into Lake Erie had been expected. In their detailed documentation of the establishment of this species in Lake Ontario, Scott and Christie (1963) expressed puzzlement at its delayed expansion in Lake Erie, which it could most likely enter through the Erie Barge Canal. They noted, however, that a small white perch was taken from Lock No. 7 of the Welland Canal (13 km upstream from Lake Ontario) in 1961 by a survey team of the Fisheries Research Board of Canada. Van Meter and Trautman (1970) mentioned the 1953 report of white perch by Larsen (1954) but did not speculate on how the species got into Lake Erie — even though they identified the Welland Canal as the most likely entry route for the alewife (*Alosa pseudoharengus*), American eel (*Anguilla rostrata*), and sea lamprey (*Petromyzon marinus*).

State, federal, and provincial fishery agencies, concerned about the impact white perch may have on other fishing resources in Lake Erie, expressed the need for more information on the abundance and range of this species. We, therefore, issued a joint request during the winter of 1974–75 to commercial fishermen of Ontario, Michigan, New York, Ohio, and Pennsylvania to save white perch taken during the 1975 spring fishing season. As a result, 34 specimens (10 females, 24 males) were collected and the capture of others was reported. Distribution of these specimens was confined to the western half of the lake (Fig. 1). In the 1975 collections 2-yr-old fish predominated (26) and 3-yr-old fish contributed the remaining number (8).

The 38 white perch collected in 1973–75 were captured with the following gear: commercial gill net, 4; haul seine, 6; trap net, 27; and experimental gill net, 1. The average total lengths of these fish were 171.4 mm ($N = 28$, range 140–194 mm) for 2 yr olds, 208.1 mm ($N = 8$, range 192–220 mm) for 3 yr olds, and 238.0 mm ($N = 2$, range 236–240 mm) for 5 yr olds. No 4-yr-old white perch were captured. Establishment of a naturally reproducing white perch population in the lake can be inferred from the sizable number of specimens obtained in 1975 and the presence of three year-classes.

The future role of white perch in the Lake Erie fish community is not known. In the Bay of Quinte, Lake Ontario, the white perch first appeared in the early 1950s. By 1960 it was the dominant species (Christie 1974). Apparently two factors favored the proliferation of white perch there: the continuing eutrophication of the Bay promoted high fish productivity, and the heavy exploitation of native piscivores permitted the prolific increase of this species (Christie 1974). Although entrophic conditions also prevail in much of Lake Erie, the presence there of large populations of such piscivores as walleye (*Stizostedion vitreum vitreum*) and white bass (*Morone chrysops*) precludes, in our opinion, development

of the white perch as a dominant species. Nevertheless, the range of the species may eventually extend up the Detroit River into Lake St. Clair and the upper Great Lakes.

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Cytotaxonomic Study of Gila Trout, *Salmo gilae*

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BEAMISH, R. J., AND R. R. MILLER. 1977. Cytotaxonomic study of gila trout, *Salmo gilae*. J. Fish. Res. Board Can. 34: 1041–1045.

Gila trout, *Salmo gilae*, has a diploid chromosome complement of $2n = 56$ consisting of 49 metacentric and submetacentric chromosomes and 7 acrocentric or telocentric chromosomes. Karyotypes of this and other species of western North American trouts of the genus *Salmo* suggest that chromosomal modifications are correlated to speciation in this genus.

Key words: salmonidae, *Salmo gilae*, karyotype, chromosome, speciation

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Salmo gilae a un complément de chromosomes diploïdes de $2n = 56$, comprenant 49 chromosomes métacentriques et submétacentriques, et 7 chromosomes acrocentriques ou télocentriques. Les caryotypes de cette espèce et d'autres espèces de truites de l'Amérique du Nord occidentale suggèrent que des modifications chromosomiques sont associées à la formation d'espèces au sein de ce genre.

Received December 30, 1976
Accepted March 14, 1977

Reçu le 30 décembre 1976
Accepté le 14 mars 1977

CHROMOSOME structure and behavior comprise an important tool for deciphering evolution, as clearly shown by the increasing use of karyotypes in evolutionary studies. Since the karyotype of a species is the physical basis of its genetic system, we are necessarily interested in the evolution of karyotypes. In the case of gila trout, *Salmo gilae*, a species limited in distribution to a few streams of New Mexico and Arizona (Miller 1972), the question of its specific distinction and of its derivation is materially aided by this first report of its karyotype.

Materials and methods — Chromosome squashes were prepared from gill tissue according to the method of McPhail and Jones (1966) as modified slightly by Beamish et al. (1971). Photographs were taken from freshly squashed preparations using phase contrast microscopy. Squash preparations were then made permanent by the method described in Beamish et al. (1971) and karyotypes were established by comparing enlarged prints with the permanently mounted preparations. All permanent preparations have been saved and are available for examination upon request.

Juvenile *Salmo gilae* were obtained from Sterling Springs Hatchery in Arizona, of which the stock came from Main Diamond Creek, New Mexico (type locality of the species).

Results and discussion — *Salmo gilae* has a diploid chromosome complement of $2n = 56$ (Fig. 1, 2d). There was some variation in chromosome number (Table 1); however 39 of the 60 squashes that were counted had a $2n = 56$ complement. The greatest number of interpretable

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Printed in Canada (J4682)
Imprimé au Canada (J4682)

FIG. 1. *Somatic chromosomes at metaphase from a 43 mm Salmo gilae.* Karyotype prepared from chromosome squash preparation. Bar represents 5 μm.

squashes was obtained from fish 3 (Table 1) and as might be expected, the largest variation in chromosome counts came from squashes from this fish. The amount of variation in counts obtained in this study should not be interpreted as being indicative of the degree that chromosome numbers vary in this species. Variation in chromosome numbers can, and probably does, result from interpretative errors caused by chromosome overlaps, loss, breaks, or chromosome additions from other squashes. Addition of chromosomes to a squash causes fewer interpretative errors, as it is often possible to differentiate such additions by the differences in the appearance of chromosomes, caused in part by differences in the amount of contraction. There were several well-spread and apparently intact squashes (Fig. 2a) that had counts higher than $2n = 56$, indicating that some variation in chromosome number probably occurs, at least in cells from gill tissue.

TABLE 1. Frequency of chromosome counts.

	Fish no.				
$2n$	1	2	3	4	Total
53					
54					
55			6	1	7
56	1	7	26	5	39
57	1	5	5		11
58			2		2
No. of karyotypes	*2*	*3*	*14*	*1*	*20*

When $2n = 56$ most squashes had 49 metacentric and submetacentric chromosomes and 7 acrocentric or telocentric chromosomes (Table 2). One good squash (Fig. 2a) had 58 chromosomes with 9 acrocentric chromosomes. Other preparations had 57 chromosomes and 8 acrocentrics, and two squashes with 56 chromosomes also had

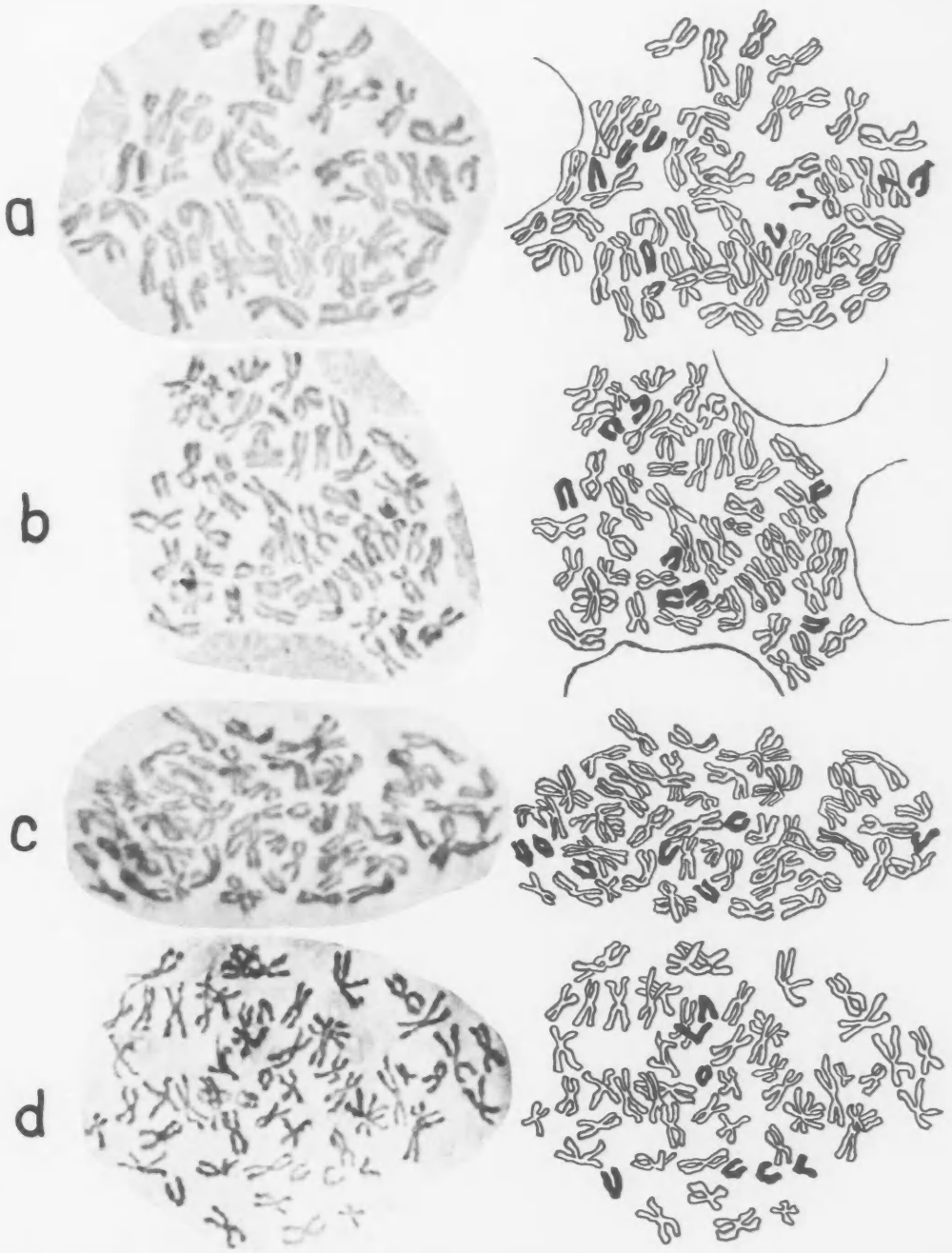

FIG. 2. Squash preparations and interpretation to show the number of acrocentric chromosomes. a, Fish 3, $2n = 58$; b, fish 1, $2n = 57$ and 8 acrocentrics; c, fish 2, $2n = 56$ and 7 acrocentrics; d, fish 3, $2n = 56$ and 7 acrocentrics. All interpretations and photographs are made from original permanent squash preparations since some detail is not apparent in the photograph.

TABLE 2. Karyotype analysis.

2n	No. of karyotypes	No. of acrocentrics	Fish no.
55	2	7	3
56	14	7	*1, 2, 3, 4*
56	2	8	3
57	1	8	1
58	1	9	3

8 acrocentric chromosomes (Table 2). While interpretive problems caused by chromosome breaks may account for some of the variation in chromosome morphology, some of the variation was apparently real. Despite this variation in number and morphology, at least one preparation from each fish examined had the modal count of $2n = 56$ with 7 acrocentric chromosomes (Table 2). The number of squashes counted or karyotyped was not constant for each fish sampled because of the varying number of divisions obtained and the varying quality of squashes.

The karyotype of *Salmo gilae* is very similar to that of *Salmo apache* (Miller 1972), but *Salmo gilae* possesses one more acrocentric and one fewer metacentric or submetacentric chromosome. This may have resulted from a pericentric inversion in only one metacentric or submetacentric chromosome. Unfortunately the four fish sampled were too small to determine if the chromosome heterozygosity was related to sex. While the presence of an apparently unpaired chromosome is unusual, there are reports of the occurrence of univalent chromosomes in fishes (Makino 1941) and chromosome polymorphism in the genus *Salmo* has been clearly demonstrated (Ohno et al. 1965; Roberts 1968). In the study of Atlantic salmon, *Salmo salar*, Roberts (1968) found a single large unpaired submetacentric in one of the stocks examined and was unable to explain its significance. Thus, the finding of an apparently unpaired chromosome for the stock of *S. gilae* used in this study is not unique.

A sufficient number of species in the genus *Salmo* from western North America have been karyotyped to allow some speculation concerning the pattern of evolution as indicated by their karyotypes. Unlike some genera, such as *Lepomis* (Roberts 1964) and *Esox* (Beamish et al. 1971), speciation in the *Salmo* may be correlated to chromosomal rearrangements. In an examination of the karyotypes of five North American species of Pacific salmon, Simon (1963), concluded that Robertsonian translocations were an important mechanism in explaining speciation in Salmonidae. There also is a definite pattern of chromosomal

TABLE 3. Hypothetical and present-day karyotypes for western North American *Salmo* species formed by Robertsonian and pericentric inversions. First number refers to chromsome number, second number to acrocentric or subtelocentric chromosomes, and third number refers to the number of chromosome arms. Boxes around karyotypes indicate present-day karyotypes of species listed below boxes. Karyotypes other than *S. gilae* were obtained from Miller 1972.

Robertsonian fusion ↓	Pericentric inversion →		
	64-22-106		64-24-104
	S. clarki		
	62-18-106		62-20-104
	60-14-106		60-16-104
			S. gairdneri
	58-10-106		58-12-104
			S. aguabonita
	56- 6-106	56-7-105	56- 8-104
	S. apache	*S. gilae*	
	54- 2-106		54- 4-104

number and morphology in the species of western North American *Salmo* that may be explained by a series of Robertsonian fusions and associated pericentric inversions (Table 3). If the karyotype of Cutthroat trout, *Salmo clarki*, of $2n = 64$ (Simon and Dollar 1963; Miller 1972) with 106 chromosome arms and 22 subtelocentric or acrocentric chromosomes can be considered to be primitive, it is possible to construct a table of possible *Salmo* karyotypes that would be derived from Robertsonian fusions and pericentric inversions or both (Table 3). The table was constructed by considering that Robertsonian fusions reduce the chromosome number by 2 and the number of acrocentrics or subtelocentrics by 4, but maintain a constant number of arms. Pericentric inversions can reduce the number of metacentric or submetacentric chromosomes by placing the centromere close to the end of the chromosome but will also decrease the number of chromosome arms. The close relationship of karyotypes among western North American *Salmo* to predicted chromosomal rearrangements is strongly suggestive that speciation is related to chromosomal rearrangements. If speciation is related to chromosomal changes, then species may have evolved in isolation rather than by crosses of two established species. If the preceding is true, species with karyotypes at the bottom and right of the table may have evolved later than species with karyotypes at the top and left of the table.

Acknowledgments — This study was supported in part by U.S. National Science Foundation grant BMS 72-02378 to R. R. Miller.

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PERSPECTIVES

Toward a Relevant Science: Fisheries and Aquatic Scientific Resource Needs in Canada[1]

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[1]This report was prepared under contract for the Fisheries Research Board of Canada. The views expressed are those of the author and not necessarily those of the Board.

Printed in Canada (J4710)
Imprimé au Canada (J4710)

Abstract

FLETCHER, H. F. 1977. Toward a relevant science: fisheries and aquatic scientific resource needs in Canada. J. Fish. Res. Board Can. 34: 1046–1074.

Recent shifts in science policy express an increased demand for scientific activities that are relevant — that will enhance the policy and management decision process for the benefit of Canadians. The implications of the increased focus on relevance to the fisheries and aquatic scientific community are discussed and measures to strengthen science in this new operating context are described.

It is concluded that an effective scientific effort will increasingly depend on the effectiveness of resource and environmental policy and planning. Arising from this conclusion is the need to develop a more orderly system of transferring scientific knowledge into the decision process. The application of applied systems analysis techniques is discussed as one solution.

It is also argued that more effective use of the knowledge of the human and social sciences is imperative to an effective synthesis of natural science knowledge. The synthesis of knowledge leading to policy or management decision alternatives can be subjected to rigorous testing against present scientific understanding or can be systematized within the constraints of existing institutional arrangements. The former describes interdisciplinary research; the latter, planning. Current perceptions of resource and environmental problems point to a need for developing interdisciplinary research programs, for strengthening the planning activity, and for establishing strong links between them. The role of the university community in interdisciplinary research is emphasized and prescriptions for strengthening this role and linkages with government and other client groups are outlined. An increased focus on interdisciplinary research in universities has significant implications in meeting educational needs for the future.

Résumé

FLETCHER, H. F. 1977. Toward a relevant science: fisheries and aquatic scientific resource needs in Canada. J. Fish. Res. Board Can. 34: 1046–1074.

De récents changements dans la politique des sciences révèlent une demande accrue d'activités scientifiques pertinentes — qui rehausseront, au profit des Canadiens, le processus de décision touchant les politiques et la gestion. L'auteur analyse les implications, pour les pêches et la communauté scientifique aquatique, d'une plus grande attention accordée à la pertinence, et il décrit les mesures visant à renforcer la science dans ce nouveau contexte opérant.

Il en vient à la conclusion qu'un effort scientifique efficace dépendra de plus en plus de l'efficacité de la politique et de la planification relatives aux ressources et à l'environnement. De cette conclusion découle le besoin de développer un système plus ordonné de transfert des connaissances scientifiques dans le processus de décision. On examine l'application des techniques d'analyse systémique appliquée comme étant une solution.

L'auteur raisonne également sur la nécessité de se servir efficacement des connaissances en sciences humaines et sociales pour en arriver à une synthèse efficace des connaissances en sciences naturelles. La synthèse des connaissances conduisant aux diverses alternatives de décision quant aux politiques ou à la gestion peut être soumise à une rigoureuse épreuve contre nos connaissances scientifiques actuelles ou systématisée dans les limites des contraintes imposées par les institutions existantes. Dans le premier cas, il s'agit d'une recherche interdisciplinaire; dans le second, de planification. Ce que l'on perçoit présentement des problèmes touchant les ressources et l'environnement fait ressortir le besoin de développer des programmes de recherches interdisciplinaires, de renforcer l'activité de planification et d'établir de solides liens entre les deux. On souligne le rôle de la communauté universitaire dans la recherche interdisciplinaire et on esquisse des moyens de renforcer ce rôle ainsi que les liens avec le gouvernement et autres groupes de clients. Le fait d'attacher plus d'importance à la recherche interdisciplinaire dans les universités a d'importantes implications sur les besoins éducationnels de l'avenir.

Received January 31, 1977
Accepted March 11, 1977

Reçu le 31 janvier 1977
Accepté le 11 mars 1977

1. Introduction

1.1 The Current Global Dilemma

At the time of writing, a notice for the second annual conference of the Canadian Association for the Club of Rome arrived. The theme of the 1976 Conference, "Long Range Planning and Consensus in the Modern Society," is highly pertinent to this study. In a descriptive commentary, reference is made to the difficulty that political structures, private institutions, and other power groups throughout the world have in ad-

justing to unprecedented challenges. It goes on to say, "One thing is certain: — if present trends are allowed to continue, mounting economic problems and social disorders will ensue at national and international levels. One alternative is to resort to imperative planning, which involves overall control and compulsion — incompatible with liberal democracy and traditional freedom. The second alternative is indicative planning, which involves active participation from private and public decision-makers on a basis of consensus and consent. But is this kind of democratic planning possible? Can it be effective in a modern society engaged in the struggle for contending appetites?"

We are perhaps on the verge of moving beyond imperative or indicative planning options to planning models that highlight the facilitating role of governments to assist desegregated, more decentralized decision-making and more direct participation by scientists in the normative process.

The issues confronting civilization are well known[2] — a burgeoning population; limited food production, storage, and distribution; depletion of resources in the face of increasing demand around the globe; and environmental degradation (Johnson 1975). The problems are basically human and social in character. The analysis of doomsayers and that of advocates of continued rapid economic growth and the "technological fix" represent two extremes in a spectrum of ideological viewpoints that, in varying degrees, influence our lives, our policy decision processes, our economy, and the effectiveness of our institutions. The fear of change and uncertainty fosters in many a strong tendency to retrench, to hold to former values and ways, and to solve new problems with old approaches and institutional arrangements. Science, along with other activities of man, is caught up in the current dilemma and the inertia of the scientific institutions has paralleled the inertia of other power structures.

This is the context in which we find ourselves: a context ripe for exploiting the intellectual and inventive capabilities of citizens toward the definition and solving of "wicked problems" (Rittle et al. 1973). Surely, in response to increasing complexity, it is imperative that scientific knowledge — both natural and social — be integrated to shed new light on such problems and on ways and means in which they might be attacked. If science is to be used effectively to enhance our ability to manage resources, we cannot continue to assume that there is an invisible wall between ecology and political science or that the benefits derived from past decades of specialization and reductionist approaches necessarily justify prime emphasis on these in the future.

[2]Well known but not well understood in a prescriptive sense. Indeed, such Malthus-like statements are too often used to justify inappropriate actions.

1.2 Purpose of the Study

The present study was undertaken for the Standing Committee on Scientific Resources of the Fisheries Research Board of Canada. The prime aim of the study was (1) to assess the overall fisheries and aquatic scientific community in Canada as to its capability to meet short- and long-term requirements and to determine if resources were being put to good use, and (2) to examine institutional and management approaches to ensure that the input of fisheries and aquatic science is being used in decision-making. The study was conducted in parallel with another by Caissie and Willmer (1976) which focused on a description of the existing situation.

This paper is strongly biased toward the thinking reflected by recent authors of studies undertaken for the Fisheries Research Board, particularly those of H. A. Regier, F. D. McCracken, R. D. S. Macdonald, G. I. Pritchard, and K. H. Loftus. It is interesting that each of these individuals has arrived at similar conclusions about the problem facing science and society. Perhaps the present author has said only what they have said already in a different way; perhaps he has added something from his analysis and experience. In any event, there is no doubt that we are all groping with a pervasive problem that deeply involves science, but that can be solved only by looking at science in relation to factors that influence science. The problem will not become fully clear as a result of studies such as this, albeit they can perhaps provide some direction; rather, clarity will result from setting processes in motion — by action, experimentation, and evaluation. As stressed in the report, there is ample opportunity to initiate such processes and to support those that have already been initiated.

2. The Science Policy System

The success of science in developing war technology during World War II and the subsequent "boom" in public demand for sophisticated technology fostered the growth of science, and within science, of specialization. The science and technology snowball has resulted in the formation of a myriad of disciplinary scientific institutions that have served to enhance communication within each specialty. During the 1940s and 50s, public expectations about the ability of scientists and technologists to solve man's problems were high;

too high — science and technology had been oversold. Partly as a result of the realization that the specialist model of science and technology could not solve many social and economic problems that were of increasing concern, scepticism about science and technology developed during the 60s. This has been fueled by the negative social and environmental effects brought about by the use of technology, a use too frequently engendered by the presence of technology rather than consideration of its impact upon society. Undoubtedly the exponential rate of increase in scientific effort (a doubling every 10–15 years in England) and the consequent cost has also had a significant bearing on the public attitude toward science and technology (MacDonald 1969). In varying degrees these factors have stimulated and fed the science debate begun in Canada by the Glassco Commission in 1960–63. In the latter part of the 1960s, the debate picked up tempo with numerous studies being undertaken. The formation of the Ministry of State for Science and Technology (MOSST) in the Government Reorganization Act of 1971, the subsequent promulgation of the Make-or-Buy policy and the Unsolicited Proposals addendum have been explicit political reactions to the "public" concern about science and technology and the various reports dealing with the subject, particularly those of the Senate Committee Special Study on Science Policy.

A major challenge of the Senate Committee was to help develop a coherent policy to enable Canada to meet its economic objectives more effectively and to more realistically face social problems. Following the Senate Committee recommendations, MOSST has given high priority to industrial and trade issues as reflected in the Make-or-Buy policy, which is designed to lower the proportion of research and development (R&D) performed in government departments and to increase it in the industrial sector.

The development of a science policy framework to define the essential roles of the federal government in the field of science has been slow in developing, largely due to the insistence by many authorities that science should be viewed apart from, rather than as part of, other activities of man. It is agreed at this point in time by the federal cabinet that science policy includes the sum of policies in three areas (courtesy of the Ministry of State for Science and Technology):

(a) Policies for the support of science, which include the support of postgraduate university research, arrangements for scientific representation abroad, the support of Canada's participation in international scientific organizations, the provision of scientifically trained man-power, the dissemination of scientific information, and the provision of certain basic research facilities by government.

(b) Policies for the application of scientific and technological resources, including policies developed within the departments and agencies for the use of science and technology in support of their objectives, policies developed through cooperative inter-departmental means for the achievement of broad multidepartmental objectives having a high technological content, and policies to govern procedures involved in the use of science and technology (e.g. Make-or-Buy policy).

(c) Science in public policy, which includes participation of scientifically trained personnel through the development of long-term national strategic policies and the introduction of scientific knowledge, analysis, and methodology into the planning activity.

Issues and problems associated with the government–university interface are currently under investigation. These include trends in employment of persons with postgraduate training, effects of inflation, and the question of indirect costs of research. The general position at the present time is that the level of support provided by the government in any particular scientific discipline, including the support of graduate students, should be responsive to forseeable demands for research trained graduates. To date, with the exception of the Make-or-Buy policy, government intentions or policies governing procedures relating to the use of science and technology resources are implicit. Many changes in respect of the announced government intentions have been initiated; however, intentions will not likely be translated into effective action until funds are made available.

2.1 The Make-or-Buy Policy

The response of the Department of Fisheries and the Environment (DFE) and the Fisheries and Marine Service (FMS) to the Make-or-Buy policy since its initiation in 1972 is shown in Fig. 1.

Commensurate with this increase in contracted research, which is primarily in the private sector, there has been a decrease (in terms of purchasing power) in National Research Council funding to universities (Fig. 2). Likewise, the support of university research through departmental grants programs has decreased (Fig. 3). To some extent this decrease in university funding through subventions and grants has been picked up through increased contracted research. However, the latter

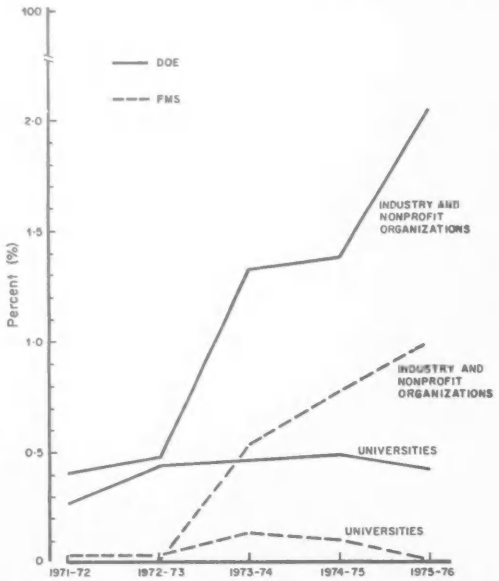


FIG. 1. R&D contract expenditures in DOE and FMS — percentage of total expenditure.

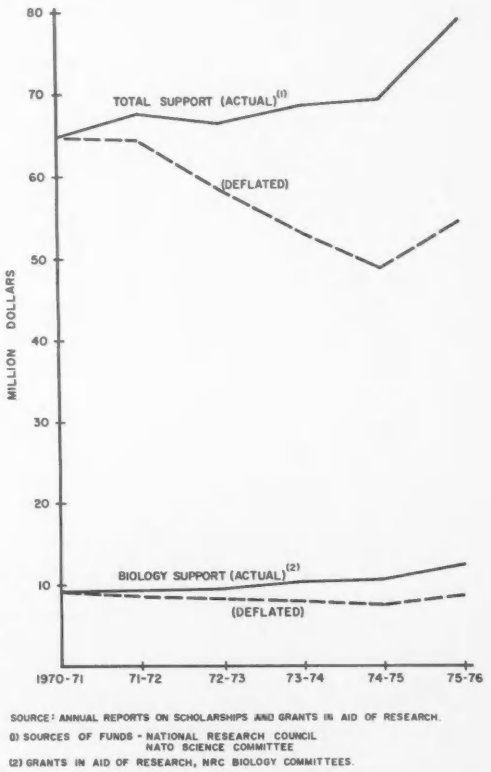


FIG. 2. NRC university research program. (Courtesy Statistics Canada — Correction for inflation using the Implicit Price Index (IPI). The IPI covers the entire range of goods and services produced and sold in the economy and is the most comprehensive of all indicators. However, it may not accurately represent the magnitude of the inflationary impact on science, but indicates the general trend.)

is primarily for applied research and technology development.

The Make-or-Buy policy concerns R&D requirements in the natural sciences to satisfy departmental R&D needs by placing contracts for them in industry (Buy) rather than by satisfying them using government employees and facilities (Make). All new R&D requirements and replacement or expansion of laboratories are covered by the policy and the decision whether or not the R&D requirement ought to be done in-house is made according to the following criteria:

(1) Where questions of security prohibit industrial involvement;

(2) Where R&D is inappropriate to industry or where no suitable industrial capability exists in Canada;

(3) Where the in-house R&D is essential to provide direct support to a regulatory function and associated planning activities and where no private firms, independent of the firms being regulated, exist or can be created;

(4) Where the in-house R&D is essential to the development and maintenance of a set of national primary standards;

(5) Where the R&D is essential to establish and maintain a limited in-house competence sufficient to assess the opportunities represented by the current state of the art, to enable departments to perform their mission and manage its contract research in industry; and

(6) Where the conduct of the R&D is necessary to the effective support and operation of in-house capital facilities that provide actual testing and research services necessary to Canadian industry.

The policy does not explicitly exclude the university community, but in practice contracts are awarded only to universities where no suitable industrial capability exists. Although the policy is a "natural science" policy, social science R&D is not explicitly excluded and some contracts are awarded for social science research.

While the policy has resulted in yet another "layer of administration" and the necessity of adapting to a set of contracting and decision procedures, it is too early yet to determine the real benefit of the policy in relation to its objectives.

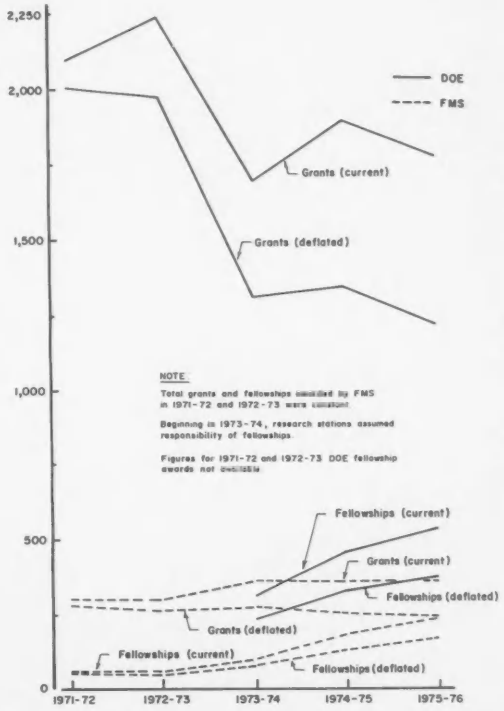


FIG. 3. Grants and fellowships awarded by DOE and FMS, 1971–76. (To provide a proper perspective, the 1975–76 expenditures for DOE represented .004% of the total budget and for the FMS .002% of the total budget. For fellowships, the comparative percentages are .001 and .002%, respectively.

The major complaint frequently voiced by federal officials during the first 2 years, was that the development and supervision of contracts required an excessive expenditure of time by departmental scientists or professionals. As administrative details have been smoothed out in departments, and particularly in Supply and Services Canada, some managers now admit that such involvement serves to clarify objectives and changes the focus of the R&D program concerned, in addition to developing useful liaison and coordination with the industrial sector. Another complaint was the paucity of expertise in the industrial sector capable of responding effectively to needs. This problem has diminished in some areas as new sources have developed and competition has increased. However, in areas where meticulous work is required, results are often disappointing or require an excessive amount of supervision.

A limit to buying as opposed to making is reached in practice as a result of financial and personnel resources consumed in developing and supervising contracts, given the need to maintain in-house R&D programs. At the Atlantic Oceanographic Laboratory, for example, one contracted project took three man-months of a senior scientist's time and virtually the full time of an engineer to initiate and supervise. Further contracts, if possible from a financial standpoint, could result in significant reductions in the in-house program.

Contracts let under the Make-or-Buy program are primarily for applied research, instrument or equipment development, or data collection. A relatively insignificant number of contracts are let for basic research. However, should a department wish, the opportunity exists to "buy" long-term basic research programs as well as large scientific programs for applied research or data collection. Still, for essential public services of a scientific nature for which the federal government is responsible, it is also civilly liable. This imposes limits to the "buying" of large programs.

The Unsolicited Proposal addendum of the Make-or-Buy policy facilitates the rapid initiation of research proposed by nongovernment organizations, particularly in the private sector, through a special fund administered by the Department of Supply and Services Canada. The fund may be used for financing unsolicited project proposals that otherwise would not be financed by a department in the current budget cycle.

2.2 University Research Support Policy

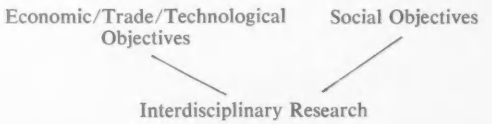
The general decrease in funding of basic research in universities has caused a considerable concern within the scientific community and has resulted in presentation of numerous briefs to the federal government. Briefs from scientific organizations and universities generally call for a return to former "real" levels of support for basic research. The toll of inflation has resulted in a real decline in actual support of basic research (Fig. 1 and 2). These points, along with arguments based on past contributions of research are contained in most briefs. However, few point to the need for evaluation and rationalization of the science concerned, or science generally, in light of the present economic situation and additional needs for science in our rapidly changing society. The context has changed and the message has not yet been widely addressed by the scientific community although individual studies such as that of the Association of Universities and Colleges of Canada (AUCC) Commission on the Rationalization of University Research (Bonneau and Corry 1972) have focused on the problem admirably.

In the federal government, steps toward rationalization of university support policies have been slow. While the current science policy emphasis is on economic development, it is notable that the proposed second phase of the Senate Committee on Science Policy — to review and recommend on social science research — has not been initiated. The need to strengthen social science research has been accepted as a legitimate aim by government, but there has been little action to support such acknowledgment.[3] Although it is the announced intention of government to stimulate interdisciplinary research, there still remains considerable confusion regarding the definition of interdisciplinary research and no formal mechanisms have been established to either encourage or support this class of research.

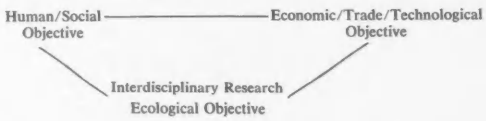
A second cause of delay in developing university research support policy is the jurisdictional issue. The provinces, which have exclusive jurisdiction over education, recognize the significant influence the federal government has on education through federal research support or purchase programs. Indeed, the provinces have for years paid the overhead for federally supported research without having a voice in the decision process. A number of provinces have developed research policies and have established grant programs that complement those of the federal government. Most are patterned after the peer or peer–management review model which adds another committee task to the load already carried by Canada's scientists.

2.3 A Deficiency in Science Policy

It is the stated intention of the federal government to introduce policies that will differentiate among the various objectives of scientific research. Science policy has to date reacted strongly to economic objectives with implementation of the Make-or-Buy policy and various industrial incentive programs. Acknowledgment has been given to the need to strengthen social science research as a means of more effectively solving the myriad of social problems that dominate today's scene. Interdisciplinary research has also been tagged for action although it is not clear that the term is used by all proponents in the same sense. The science policy framework that appears to be emerging, then, might be represented as follows:



If this representation has any validity, it exposes a startling omission that has been overlooked by biological and environmental groups in their interventions on science policy development. Surely, if government is to introduce policies that reflect various objectives of scientific research, the objective of understanding natural ecosystems and man's impact upon them deserve explicit policy recognition. The importance of such policy statements cannot be overemphasized; they have profound implications for the development of scientific programs in the environmental and resource management fields and for the support of related research. In addition, as illustrated below, the inclusion of an ecological objective in the science policy framework and the elevation of the social objective would add more meaning to interdisciplinary research, at least as this class of research is defined in the Canada Man and the Biosphere program (Canada MAB 1975) and used in this report.



The development of a science policy recognizing an ecological objective for scientific research is considered a key requirement for developing an effective fisheries and aquatic science system.[4] If ecological objectives are not soon seen to be at least as important as social objectives, then it is virtually inevitable that we will continue to move to a point where the former will become more important than the latter.

The above model is a logical one for policy development. If science is to be applied to policy development (page 1049) in a way that recognizes the nature of the current dilemma, surely it must be applied in an integrative framework rather than that of the traditional disciplinary one best described as reductionist. In this paper, the relevance of science is discussed in terms of such an integrative framework.

[3]Social science research and development, as a percentage of the federal R&D dollar, has increased from 7.1% in 1971–72 to 12.1% in 1975–76. In terms of purchasing power, 1971–72 levels have not been maintained.

[4]The establishment of the Natural Environment and Research Council (NERC) in Great Britain in 1965 under the Science and Technology Act represented an explicit policy recognition of a need to know more about the ecophysical system.

3. Implications of Science Policy for Fisheries and Aquatic Sciences

The terms of reference for the present study called for an assessment of scientific resources and their capability to meet short- and long-term commitments. Early in the study, it became evident that such questions could not be properly addressed within existing frameworks, as exemplified by traditional institutional arrangements, planning and supporting information systems. These have not changed sufficiently as yet to reflect current perceptions of resource management problems and the ways and means whereby such problems might be tackled (Chevalier et al. 1972; Friedman 1967). The latter, of course, involves the development and transfer of knowledge and here, the "institution science" itself must be viewed as part of the changing scene.

In the foregoing section, the science policy system was described in some detail. One of the prime science policy foci is on relevance. In a relevance context, we might view the primary function of scientific activities applied to the fisheries and aquatic science mission as being the development and use of knowledge to produce improvement in resource and environmental policy and management. The scientific objectives here must relate to both short and long time frames. For the former, the use of existing knowledge dominates; for the latter, the filling of knowledge gaps through gaining a better fundamental understanding of pertinent human, social, economic, and ecophysical systems is imperative.

3.1 Relevance

The connotation of relevance is changing. From the viewpoint of the scientist, the feeling that he/she was relevant has depended more on peer acceptance than on evaluation based on contributions to policy or management decisions. Organizational separation of research functions from other activities of departments is the preferred traditional model of scientists. Longer range research activities — and long range planning, for that matter — are difficult partners for those who are preoccupied with today's problems. The planning–budgeting–evaluation and supporting information systems and the reward structure naturally favor short-term activity (Vickers 1967). Traditionally, these have been separated; either institutionally as in the case of the former Fisheries Research or Defence Research Board laboratories, or within a department when the size and type of research effort has justified internal separation, as Agriculture Canada.

Much, if not most, scientific research in government laboratories is conceived by the scientist and "sold" to management. This has been termed a "bottom-up push" situation (Wynne-Edwards and Neale 1976). This is not to say that the research is not relevant; rather, it is a matter of degree. The research conceived by the scientist has been determined largely by scientists in the context of their perception of things. Certainly, it can be argued that many benefits and much progress have been made using this model. But, if science is to be "relevant," both in terms of today's and tomorrow's problems — and this is what science policy is saying — the selling job by scientists, which reflects a valuable perception of things, must be handled as feedback into a well-ordered resource policy–management–decision process, a process that defines knowledge gaps in terms of human and social needs (refer Section 2).

3.2 Signals of Change

It seems apparent, then, that new demands are being made of scientists and of those involved in the transfer, synthesis and use of knowledge (Gregory 1975). The opportunity for meeting such new demands is ripe in the fisheries and aquatic areas, given the mix of problems, perceptions, and changes taking place. Hence, the answer to the question of whether or not scientific resources in the fisheries and aquatic area are capable of meeting short- and long-term commitments cannot be answered realistically in terms of past accomplishments or present momentum. Answers based on information systems that still reflect past perceptions of the needs for science and hence the disposition, use, and classification of scientists would be tantamount to ignoring rapidly changing reality. The data can, of course, assist in understanding the current context and expose deficiencies, once an appropriate context has been described that reflects the changing condition. In an assessment of scientific resources, then, there is need to develop a framework that reflects the realities of science policy, organizational changes, resources management perceptions and new perceptions of scientific enquiry, to name a few. To define this framework is to define also new institutional needs, management modes, evaluative criteria, and scientific information system formats whereby the interfacial barriers between research and operations and science and the policy–decision process can be reduced.

In fisheries, the decision in 1973 to bring the Fisheries Research Board laboratories into the Fisheries and Marine Service (FMS) as an inte-

gral part of the in-line system reflected a policy prescription for making science more relevant. The recent reorganization of the Service has been slow, partly because of the difficulties in resolving questions concerning the organization of research and related scientific activities. Nevertheless, the die has been cast for the time being at least. It has been assumed that close organizational ties between scientific and operational groups will facilitate improvements in both science and fisheries management.

The current mix of circumstances in the area of fisheries appears to have the right ingredients to foster development of new approaches. Firstly, the problem of fisheries management is critical in an ecological, socioeconomic, and institutional sense. Secondly, it is widely acknowledged that a new approach to management is required to replace the traditional one based on knowledge of species. Thirdly, the problem and the need for new approaches coincide with the changes wrought by a decade of science policy debate. Finally, the melding of two scientific groups, fisheries and oceanography, can provide the basis for developing approaches leading to a better understanding of our aquatic environment.

3.3 Pattern of Change

To meet the demands of science policy, both scientists and nonscientists alike will need to alter former ways of thinking. Traditional views of scientists that creativity and innovation require freedom in the form of certain institutional independence from operational activities and objectives is being challenged. Operational staff will not take easily the imposition of direct "scientific" intervention into their traditional ways of doing things. The strong tendency of scientists to shy away from prediction until "more information is procured" will have to be balanced with the tendency of operational people to "shoot from the hip" to meet real world demands. This science policy experiment — as it might well be termed — raises interesting questions about information transfer and organizational arrangements. Effective melding of scientific enquiry with operational reality — theory and practice — may well depend on acceptance and use of new approaches designed to deal with complexity. Certainly, there is a growing literature dealing with "scientific" enquiry systems (Kuhn 1970; Maruyama 1973; Mitroff and Pondy 1974; Popper 1959; Rhyne 1971). Nor is there difficulty in finding examples of attempts to apply such theory in addressing real problems (Chevalier 1969; Chevalier et al. 1972; Gibbons and Voyer 1974; White and Gates 1974). However, traditional organizational arrangements reflect traditional concepts and are not on the whole responsive to such new approaches to enquiry. Hence, examples of the application of such approaches are partial and sporadic.

There is, of course, a whole class of methodology that is applicable here and that is most frequently referred to as applied systems analysis in its application. Some words of caution are in order, however, since this term often means different things to different people. As Regier (1976b) has emphasized, there is need to distinguish between systems analysis as used in developing ecosystem models, and applied systems analysis as interpreted, for example, by the International Institute of Applied Systems Analysis (IIASA), in the Man and the Biosphere Program, and the Institute of Animal Resource Ecology at the University of British Columbia (U.B.C.). The latter "holistic" interpretation is pertinent to the discussion later in this report. Furthermore, it is stressed that applied systems approaches are not limited to mathematical manipulation of computerized models, but include a host of "soft" approaches developed largely in the field of psychology and sociology and applied in the field of marketing, management, and planning. While a number of these techniques have been applied as "teaching" tools within the Fisheries and Marine Service or the Department of Fisheries and the Environment, none has been applied as an integral part of the decision process; for example, simulation techniques developed by the Institute of Animal Resource Ecology at U.B.C. have not been widely used within the Department. A further example, in a policy research setting, is found in the Westwater Research Centre at U.B.C. where an ordered scientific synthesis of knowledge and information from both natural and social science areas has culminated in conclusions on water quality management in the Lower Fraser River (Dorsey 1976; Swainson 1976).

Such holistic approaches are viewed with some skepticism by scientists and decision-makers alike. In part, this is due to lack of understanding, in part to a natural tendency to hold on to old and tested ways and enquiry systems, in part to current institutional arrangements and management systems and a lack of knowledge of management and the management sciences.

3.4 Institutional Factors

Organizationally, some moves have been taken in FMS to link science more closely with the resource management decision process.

Currently, in FMS, the traditional model, in which research and operations are institutionally

separate, has been dropped by the absorption of the FRB laboratories into the Service. In both Fisheries Management (FM) and Ocean and Aquatic Sciences (OAS) the logical interpretation of the traditional model would be for research units to report through regional scientific directors-general (D.G.) to a central scientific assistant deputy minister (A.D.M.). In the present organization, research units in FM report through a regional D.G. who has responsibility for science and operations to an A.D.M. who also has these dual responsibilities. In OAS, regional D.G.'s report to a central A.D.M. who has both scientific and operational responsibilities.

Also, there have been moves to more effectively involve scientists in the decision process; for example, the proposed establishment of a scientific advisory committee in the Atlantic region to review and interpret scientific information and data for managers responsible for allocation decisions. There remains, however, some skepticism among scientists about the outcome of recent changes.

In the many interviews with scientists across the country during this study, it was quite apparent that much remains to be done to provide scientists with that very necessary feeling that they are relevant. The most common complaints focused on lack of central policy direction, lack of dialogue with senior executives in Ottawa, lack of involvement in planning and priority setting, lack of freedom for research managers to manage, the obscurity of the rationale for central and regional decisions, and the increasing demand for scientists to become involved in short-term, problem-solving activities. On this latter point, most acknowledge that such involvement was stimulating and useful in fostering more effective research and indeed, most have been involved in both over time. However, there was an obvious feeling among many that there was a danger of moving too far in this direction to the detriment of longer term research devoted to understanding of the mechanisms responsible for observed effects.

These responses corroborated an earlier conclusion that the interface between scientists and those responsible for operations and resource management and policy decisions was the most significant barrier to effecting improvement in the scientific effort in FMS. Also, it was apparent from observations made during this study, that other problems which were identified, such as management of research, research duplication, information systems, training and resource needs for the future, would be adequately addressed as incidental to the process of breaking down this barrier.

To break down the barrier, however, demands substantive changes in not only science, but also in the planning, management and policy decision, and supporting administrative processes. From the foregoing, it is evident that the relevance of science appears to be increasingly dependent on the relevance of policy and management decisions. While the move in FMS to more closely link science and resource management–policy may be viewed with some skepticism for reasons already noted; such skepticism can be justified only if steps are not taken to create a more responsive planning and management–policy decision system. A prime need is for the introduction of applied systems analysis methods to facilitate the ordered transfer of scientific knowledge into the resource planning–management–policy decision process. The integral involvement of scientists in the latter process would do much to provide scientists with a deeper understanding of objectives and rationale and what is required of them — a need not met through dry directives arising from current management by objectives (MBO) strategy (Chevalier and Burns 1977).

The introduction of ordered approaches to more effectively link science with the resource management and policy development areas can be more readily instituted within organizations that have direct management and policy, as well as scientific responsibilities, than where this is not the case. FMS has sole or primary federal responsibility for management and policy in the areas of harvest management, aquaculture, and utilization. For other resource and environmental management concerns, responsibility is shared with other services, departments, and governments. For example, FMS shares responsibility with other services and governments for aquatic environmental quality and recreation. Other areas to which resident scientific acumen contributes include ocean resources, transport, weather and climate prediction, and national security. An institutional mandate will limit, then, the extent to which systematic approaches to link science and the policy and management decision process can be readily applied. However, if, as is argued here, the relevance of science demands evaluation in accordance with policy and management decision criteria, it can be expected that new mechanisms and institutional arrangements must evolve to facilitate a more orderly transfer and evaluative process (Regier 1976a). Indeed, there have been a number of initiatives in this direction, including comprehensive river basin planning resulting from the promulgation of the Canada Water Act, various environmental assessment programs such as the MacKenzie River and Beaufort Sea, and the development of an oceans policy.

In the following section, illustrations are provided to show where use of applied systems ap-

proaches might facilitate the flow of scientific knowledge into the policy and management decision process and hence lead to a more relevant scientific effort.

4. Ordering a System

As noted above, it is easier to develop effective links between science and the management and policy decision process in areas where both the science and the policy responsibilities lie within one agency (Environment Canada 1975). This applies in the areas of harvest management, aquaculture, and utilization. For aquatic environmental quality and estuarine and coastal management, responsibility is shared. The following sections deal with both classes and serve to illustrate where applied systems approaches might be used to increase the effectiveness of the scientific effort in these important scientific areas. While some illustrations focus on policy development, some on resource management, and some on both, the emphasis does not imply that other parts of each system do not require attention.

4.1 Harvest Management

It is generally acknowledged that management based only on a stock-by-stock assessment, reflecting a biologically defined maximum sustained yield concept, is grossly inadequate. Increasing emphasis is being given to a socially defined optimum sustainable yield as a more appropriate concept (Roedel 1971). This shift in emphasis is in harmony with science policy shifts and shifts in perceptions of resource management problems, albeit these are both largely still in early development stages and hence ill defined.

The major objective of science in the harvest management system is usually perceived as food production. The call for a move toward an optimum sustainable yield concept has implications that reach beyond the food objective to include a social objective of enhancing the lives of fishermen and of preserving cultural identity. The optimum sustainable yield concept implies the need to extend the food objective to include a sociocultural objective. Inherent in both the food and social objectives is an environmental objective. The relevance of science must be evaluated in the light of all three objectives.

The need to integrate socioeconomic and ecological factors into the decision model raises three questions: how might this best be accomplished, where is the social science research backup, and what institutional arrangements might best support such integration?

From a scientific viewpoint, it could be said that the best way to accomplish this is through some well-ordered approach that will ultimately lead to the development of testable hypotheses. Thus, the objective of a supporting scientific mission might be described as the development of an holistic and scientific approach to harvest management. The term "holistic" has been inserted to stress the need for integration of both biological and social parameters which bear on problems requiring decisions for palliative action. Thus, the recognized need to integrate ecological and social factors in a more ordered way to enhance decision-making for harvest management calls for priority emphasis on methodology. The criteria for choice of method to facilitate a link between research operations and decision-making and between the natural and social sciences are, in a general sense, fairly straightforward.

Firstly, drawing on the Kantian maxim that experience without theory is blind, but theory without experience is merely intellectual play, the method should facilitate the testing of both.

Secondly, recognizing the dangers of misinterpretation of scientific knowledge in the transfer process and in the application of knowledge, the method should allow for the integral involvement of scientists — both natural and social — with those involved in practice and are responsible for decisions. The benefits of synergism are also inherent here.

Thirdly, order and rigor are imperative. The time-honored method for participatory information synthesis — the committee — may be less discomforting than one in which individual input is exposed in depth and tested against that of others. The committee, in its usual operating mode, is time consuming and can hardly be considered as the ultimate method for effective information transfer and synthesis, let alone a basis for developing and testing hypotheses.

Finally, a criterion of both choice and use relates to expectations. Given the complexity of the ecosocial system, obviously no method can provide the basis for precise decision; rather, the method must be viewed as a learning process that will, on the one hand, aid and abet decisions over time and, on the other, identify knowledge and intelligence needs and priorities.

Introduction of knowledge transfer methods that adhere to these criteria are critical to the realization of the full potential of scientists and to the maintenance of an appropriate balance between long- and short-term scientific pursuits. Based on the probable truth that a baby does not learn to walk by contemplating the action in his crib, a start should be made to initiate applied systems approaches, even though the first steps will result in some falls. Several possibilities exist.

4.1.1 *The Gulf of St. Lawrence project* — Considerable effort was expended on planning the Gulf of St. Lawrence study. Initially, it was conceived by scientists as an appropriate scientific thrust to put bits of physical and biological knowledge together — a move to develop some better understanding of cause and effect. The concept appealed to others with different interests and the project expanded to include stock assessment and finally, social parameters (McCracken and Macdonald 1976). Perhaps it was fortuitous that funds were not made available for continuation of the project. To the physical and biological scientists, and to some social scientists, the objectives of the project were obscure, the project was too all-inclusive and hence, too big to be manageable. Even so, it provided a legitimizing umbrella to justify pursuit by scientists of their special interests and was thus cautiously supported by them. It would be useful to review the proposal in light of the above discussion and in light of current initiatives and concerns. For example, the introduction of total allowable catch (TAC) has introduced a resource management concept that augers a significant shift in use of common property resources. Further, McCracken and Macdonald (1976) and Regier (1976c) have indentified the inshore or hinterland problem and called for unique planning, policy, and management approaches. Also, Coastal Zone management is becoming necessary and various initiatives (Canada MAB 1976) have been taken toward grappling with coastal problems in a comprehensive way, as was the case for river basin management almost a decade ago. Such initiatives and concerns, together with the need to test various alternatives to conventional decision and management modes, and to introduce new ways of linking science with "doing" as discussed herein, are highly pertinent to a truly comprehensive Gulf of St. Lawrence study.

Judging from the initiatives already taken, the interest engendered, and the potential for developing and testing an holistic approach, every encouragement should be given to a renewed planning effort for the Gulf Project.

4.1.2 *The salmon enhancement program* — A second possible contender for an holistic scientific approach to harvest management is the salmon enhancement program on the west coast. Here, a strong resource commitment has been made in support of the program. Simulation modeling has been employed as a learning tool through the Institute of Animal Resource Ecology at U.B.C. The program could not as yet, however, be considered as integrated. Various impressions were gained about the program from fisheries researchers and operational personnel during the course of this study and they must be considered if an integrated approach is to be taken, for example:

— researchers are fearful that existing knowledge and historic data might be misinterpreted by operational staff;

— researchers are concerned that experimental programs are not scientifically sound (hypotheses, experimental design, and observational needs);

— operational people feel quite competent to proceed with minimal involvement by researchers;

— the enhancement program is being used by many participants as an umbrella to pursue their pet projects with the result that coordination and integration are impaired and the program in reality consists of a large number of discrete activities "spread all over the B.C. map";

— there is considerable concern that initial success may lead to ultimate failure since there is insufficient knowledge about the carrying capacity of the ocean range, particularly in light of U.S. and Japanese sea-ranching programs;

— insufficient knowledge exists regarding the longer term impact of introduced stocks on natural stocks to justify a program involving so many spawning rivers; and

— resource conflict must be resolved by confrontation; there is little interest in a long-range strategy to find alternative ways to resolve conflict.

These observations represent honest opinions by legitimate actors in the system. Can the validity of such opinions be tested by initiating an applied systems approach? Would such an approach lead to more effective use of scientific resources? Would more effective bi- and multilateral agreements result from such an approach? The answer to these and similar questions should be affirmative.

4.1.3 *Lake management* — Perhaps both the easiest and the most difficult situations in which to initiate an applied systems approach are found in the freshwater areas. Small lakes lend themselves admirably to integrated management approaches. Indeed, there are numerous examples of experimental management approaches using lakes in which sufficient control can be exercised to facilitate scientific design (Loftus 1976). The expansion of existing experimental management programs to include more social science input would serve to enhance the development of the applied systems on the broader front.

The Great Lakes, particularly Erie and Ontario, perhaps pose the most difficult problem of all in holistic management. Because of the jurisdictional, institutional, use–demand situations, pollution aspects, and, in general, the pressure of

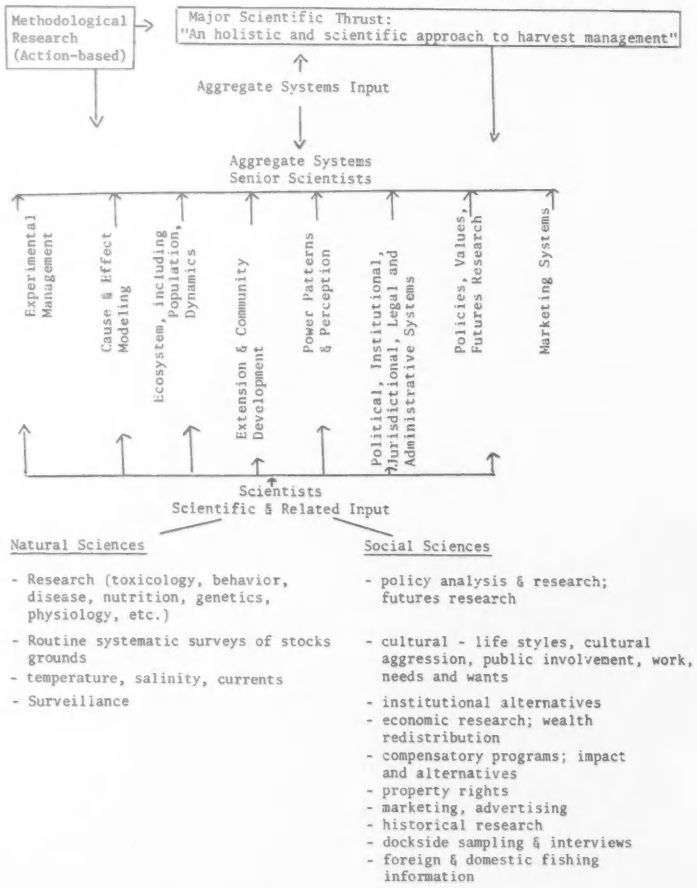

Methodological Research (Action-based)
Major Scientific Thrust: "An holistic and scientific approach to harvest management"
Aggregate Systems Input
Aggregate Systems Senior Scientists
Experimental Management
Cause & Effect Modeling
Ecosystem, including Population, Dynamics
Extension & Community Development
Power Patterns & Perception
Political, Institutional, Jurisdictional, Legal and Administrative Systems
Policies, Values, Futures Research
Marketing Systems
Scientists
Scientific & Related Input
Natural Sciences
- Research (toxicology, behavior, disease, nutrition, genetics, physiology, etc.)
- Routine systematic surveys of stocks grounds
- temperature, salinity, currents
- Surveillance
Social Sciences
- policy analysis & research; futures research
- cultural - life styles, cultural aggression, public involvement, work, needs and wants
- institutional alternatives
- economic research; wealth redistribution
- compensatory programs; impact and alternatives
- property rights
- marketing, advertising
- historical research
- dockside sampling & interviews
- foreign & domestic fishing information

FIG. 4. Science for harvest management.

the megalopolis on the system, it is a poor one to initiate the first faltering steps toward integrated management. Yet, it also offers the greatest challenge, since the complexity demands that fisheries and aquatic quality be considered in light of the many other demands on the system, i.e. as a subsystem of the broader water and costal management systems. Perhaps the only organization that could successfully initiate and coordinate an holistic management thrust at present is the International Joint Commission (Anon. 1973: Can.–U.S. University Seminar 1971–72, Cornell Univ.).

Experimental management has been referred to above. It is generally recognized that the solution to many of the problems of harvest management must be solved by drawing on inferences derived from controlled experiments. To date, experimental management has been impeded primarily by the wide gap between scientists and those responsible for harvest management decisions, a problem being considered in the present study. There is need for continued pressure on policy makers to assign specific areas for experimental management purposes, as emphasized by Regier (1976c). Experimental management is considered a prime component in the framework being developed. This and other elements, explicitly noted or implied in the foregoing discussion, can be put together along the lines shown in Fig. 4.

For each of the aggregate systems shown — and these are illustrative — a systematic synthesis of pertinent scientific knowledge drawn from the scientific and related activities listed would provide input into the proposed synthesis. The need for systematic synthesis here is emphasized; the aggregate systems also demand the use of systematic synthetic techniques, involving a team and, in most cases, several disciplines or special-

ists in the areas identified in the figure. Those responsible for each aggregate system, preferably senior scientists, would be integrally involved in the ordered decision process.

As noted, applied systems analysis techniques are not well developed in an operational sense. Hence, there is need for a methodological research team to be involved in the process, as shown in Fig. 4. This team should include, along with expertise in mathematical manipulation and ecology, competence from the field of psychology or social dynamics.

4.1.4 *Social science backup* — In the holistic approach proposed it should be expected that the contributions from the social sciences be justified by a body of theory and observation equal to that provided from the natural sciences. This may not be easy, however, for three reasons. Firstly, while there has been a long tradition of natural science research backup in resource departments, this has not been the case for the social sciences. Secondly, the main thrust of natural science research has been that of developing an understanding of the mechanisms responsible for observed effects and the testing and application of such knowledge in innovative ways. The primary objective of social science research in government, on the other hand, has been in applied research, toward improving policy, management, instrumentalities, etc., within the existing structural framework (Triste 1969; Sewell 1975). The opportunities to test hypotheses and to innovate are seldom accorded and, in instances where they are, they are not testable in the same way, or in the same time frame, as are hypotheses of the natural scientist. Finally, the enquiry systems that appear most appropriate for innovative social science research are neither acknowledged as scientific nor often understood by natural scientists (Boulding 1956; Kuhn 1970; Mitroff and Pondy 1974). Parenthetically, it should be noted here that this is true of many social scientists, since there has been a tendency for the latter to adopt the enquiry systems of the natural scientists (Boulding 1956). In any case, the requisite social science backup will not likely be provided from within the Department in the short-term. Rather, it must be sought in the university community, as will be discussed in a following section.

This leaves the third question, "what institutional arrangements might best support an holistic and scientific approach to harvest management?".

4.1.5 *Institutional aspects and management implications* — Regier and McCracken (1975) have described an organizational structure in relation to the kinds of information and processing required for decision-making. This description, as modified by Ketchen (1976) to conform closer to organizational realities, is shown in Fig. 5. The focus of this structure is on the natural sciences, even though Regier and McCracken have emphasized the need to more effectively use knowledge derived from the social sciences in the decision process. The structure recognized the need for synthesis and modeling at the research level, which conforms with the aggregate analysis groups in Fig. 4. Figure 4 could infer that those responsible for the synthesis of research information — usually at the director level[5] — should, along with their counterparts in the monitoring unit and from other pertinent research programs (Fig. 5), be prime participants in the holistic approach proposed herein. In keeping with this approach, the Scientific Services and Management Centres would logically be merged.

A further modification would seem in order. In view of the importance of ensuring that international negotiations are conducted in full cognizance of the inferences gained through the proposed holistic approach, there should be a closer relationship — an involved relationship — between the International Fisheries Directorate and the Management and Scientific Services Centres. Figure 6 shows the changes suggested which conform to the present analysis.

4.1.6 *Management aspects* — The proposed approach also has a number of implications for the management of scientific programs. A key criterion for the choice of managers (both scientific and resource) should be a clear understanding of, and identification with, applied systems approaches. Other criteria, drawn from a departmental study in 1975 (Policy for Canada's Commercial Fisheries, FMS, Environment Canada) have been noted by Caissie and Willmer (1976). Apart from the almost incidental exposure of Fisheries and Marine scientists to such approaches as that of the Animal Resource Ecology Institute of U.B.C., or in a few cases to IIASA, little opportunity exists for scientists to gain a deep understanding of applied systems techniques; many have done so, but only through fortuitous circumstances or their own effort. In fact, no training programs have been identified that would provide the requisite understanding in the context of resource management, short of spending a year working with one of a relatively limited number of university groups, for example, at the Institute of Animal Resource Ecology and the Westwater

[5]Here, the involvement of senior scientists would be appropriate, given the heavy administrative load of executive staff.

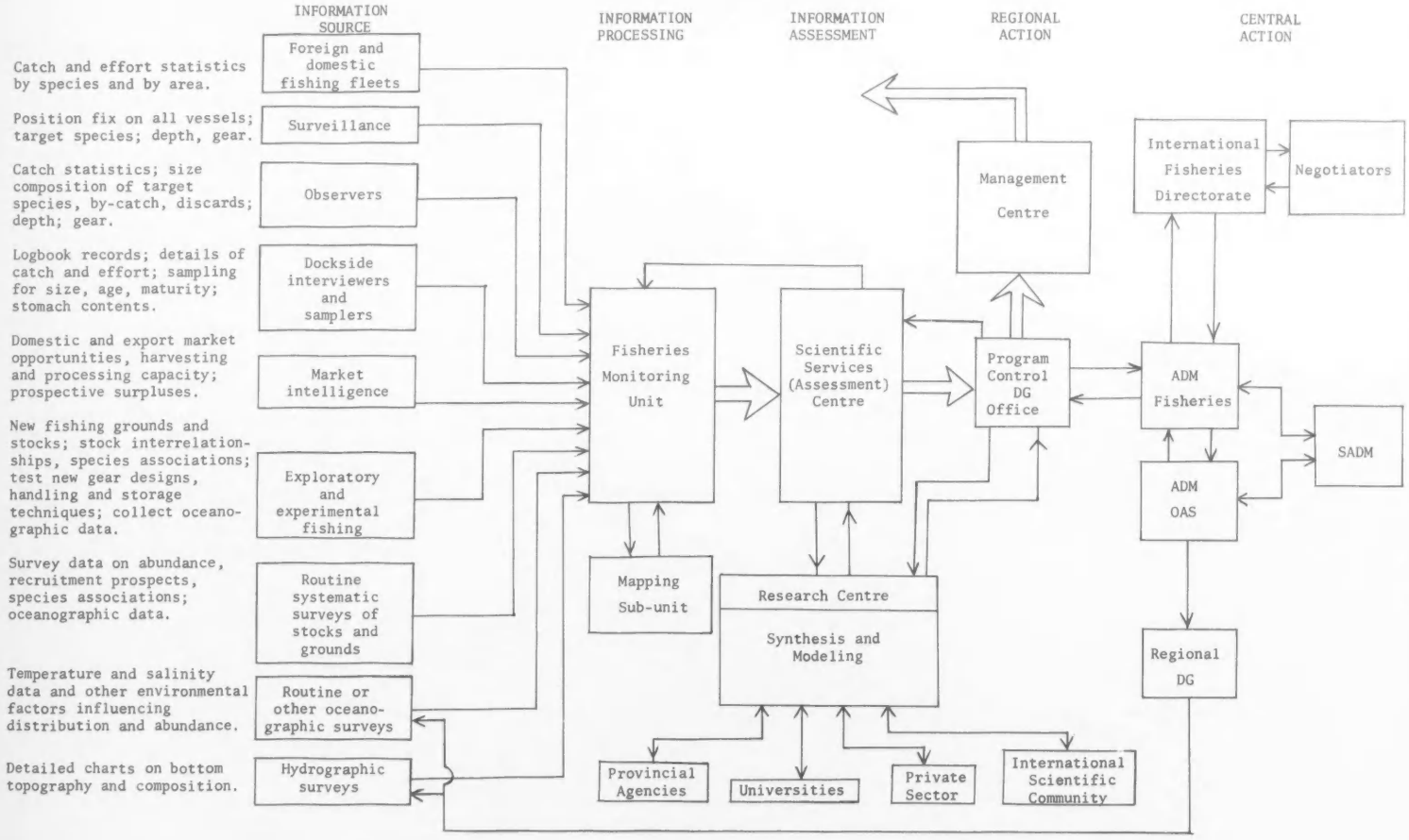

INFORMATION SOURCE
INFORMATION PROCESSING
INFORMATION ASSESSMENT
REGIONAL ACTION
CENTRAL ACTION
Catch and effort statistics by species and by area.
Foreign and domestic fishing fleets
Position fix on all vessels; target species; depth, gear.
Surveillance
Catch statistics; size composition of target species, by-catch, discards; depth; gear.
Observers
Logbook records; details of catch and effort; sampling for size, age, maturity; stomach contents.
Dockside interviewers and samplers
Domestic and export market opportunities, harvesting and processing capacity; prospective surpluses.
Market intelligence
New fishing grounds and stocks; stock interrelationships, species associations; test new gear designs, handling and storage techniques; collect oceanographic data.
Exploratory and experimental fishing
Survey data on abundance, recruitment prospects, species associations; oceanographic data.
Routine systematic surveys of stocks and grounds
Temperature and salinity data and other environmental factors influencing distribution and abundance.
Routine or other oceanographic surveys
Detailed charts on bottom topography and composition.
Hydrographic surveys
Fisheries Monitoring Unit
Scientific Services (Assessment) Centre
Management Centre
Program Control DG Office
International Fisheries Directorate
Negotiators
ADM Fisheries
SADM
ADM OAS
Regional DG
Mapping Sub-unit
Research Centre
Synthesis and Modeling
Provincial Agencies
Universities
Private Sector
International Scientific Community

FIG. 5. Information flow and synthesis in the harvest management system.

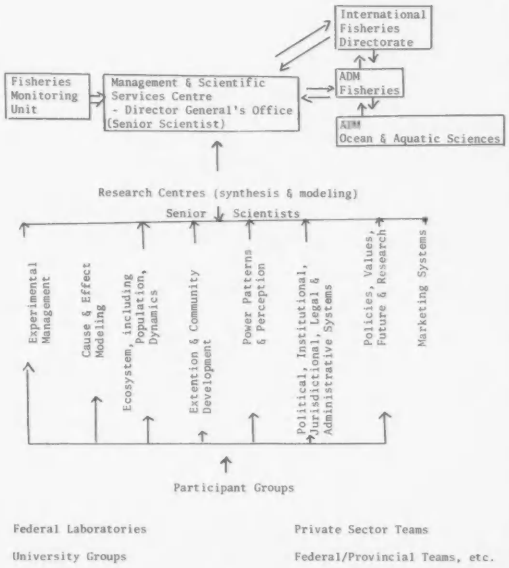


FIG. 6. Modified organizational structure.

Institute at U.B.C., and the Environmental Studies Faculty at York. Bits and pieces can be picked up at numerous universities — in environmental faculties, resource management programs (e.g. universities of Guelph and Manitoba), departments of psychology, marketing, political science, business administration, history, and philosophy — and in some management training programs such as the International Management Development Program (Geneva). The Tavistock Institute of Human Relations in the United Kingdom has developed an approach that is particularly pertinent but is not a training program in the normal sense. If the assumption that the lack of an applied systems approach to harvest management is the key need in our attempts to more effectively use scientific information and scientists in the allocation decision process (i.e. relevantly) and to break down the barriers between scientists and those responsible for operations and policy and management decisions, steps should be taken to develop training programs in applied systems analysis for present managers, senior scientists, and those who aspire to management or senior scientist positions, and to encourage participation in such programs. This is discussed further in Section 5 in reference to the university community.

Earlier mention was made of the need for changes in perceptions of scientists as requisite to breaking down this barrier. This will not likely be accomplished in the short term. In the area of scientific management, a quote from Sir Henry Tizard (Clark 1975) emphasizes the nature of the problem and the need for focusing attention on longer term policy:

"Scientific men are usually indifferent administrators and seldom men of the world. They should not be expected to undertake tasks for which their expertise and training have not fitted them. It is wasteful to turn a first-class scientist into a second-rate administrator. Administration is a job for people who have been trained to administrate, but if they are to administrate scientific activities they must have had a broad general scientific education. I cannot see that this is impossible, though I admit that it is a long-term policy."

4.2 AQUACULTURE

Aquaculture is presently a tag-along activity of the more dominant harvest management thrust. Pritchard (1976), in his call for an integrated approach toward structured aquaculture development, stressed the need for development of an aquaculture policy and the formation of an attendant infrastructure. The scheme proposed, which was adapted from one developed by Jantsch (1972), is supportive of the approach proposed above for harvest management and provides a logical framework for management of research and information.

More effective use of the scientific knowledge and of scientific resources pertinent to aquaculture development must be preceded by development of policy and an appropriate infrastructure. Initiatives have been taken toward policy development and a 5-year plan has been initiated by Environment Canada to strengthen the technical and economic base of commercial aquaculture. This action is in response to an increasing interest in aquaculture in Canada, and hence, will not likely be offset by counterpressures from those who would prefer to have present limited resources allocated elsewhere. Nevertheless, such counterpressure provides incentive to effective system design. The design proposed by Pritchard conforms to the approach developed in this paper and addresses the prescribed need for providing an effective formal organizational relationship between science and those responsible for operations and resource management and policy decision. To complete the picture, a methodological relationship must also be put into place, a point that the present author contends was not stressed strongly enough by Pritchard, although he did note the need for a transdisciplinary approach and the need is explicit in the model proposed (Fig. 7). It is emphasized herein that *both* organizational and methodological aspects must go hand in hand in the development of a science manage-

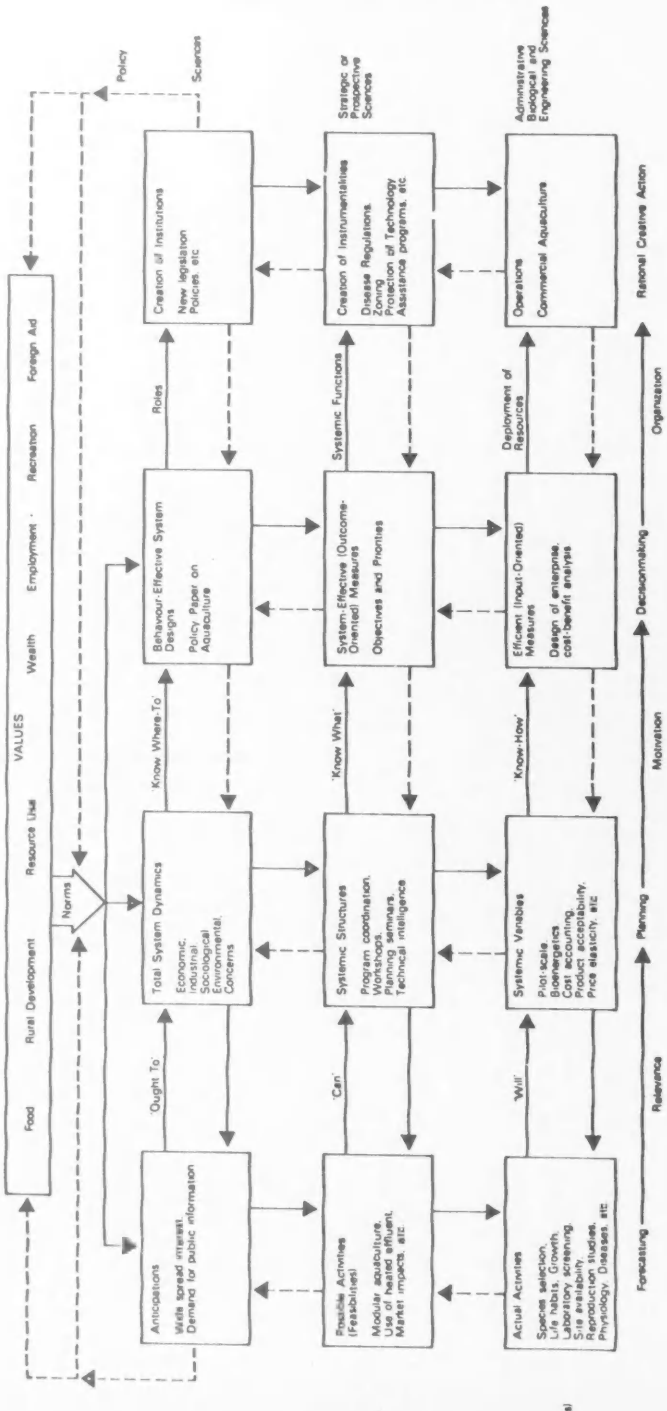


FIG. 7. Structured aquaculture development.

ment system that will conform to science policy dicta, new perceptions of resource problems, and management solutions. Development of an aquaculture policy should then be accompanied by appropriate institutional adjustments (Pritchard 1976) and the introduction of an applied systems methods. Gaps in the present research program have been identified by Pritchard as falling into three areas, viz policy, strategy, and operations. Almost all of the present research effort directly or incidentally related to aquaculture is at his operational level. The need for an increase in research effort at the policy and strategy levels, as outlined by Pritchard, again emphasizes the need for involvement of the social scientist.

The bottom two blocks in the left of Fig. 7 correspond to Fig. 4 and 6 with the "systems structures" block corresponding to the holistic and scientific approach proposed in this study. The Jantsch model carries the case further and illustrates a possible series of structures and interfaces that would serve to eliminate the "bottom-up push" while still ensuring that perceptions of scientists were objectively considered in the policy decision process.

4.3 Utilization

The utilization subsystem covers the activities from harvest to consumption (preservation of quality, processing, product development, and marketing) and consequently science must serve the client interests of the fisherman or aquaculturist, the processing industry, the wholesaler, retailer, and the consumer. Since the activities of the clients are interdependent, one might expect the scientific activities that serve them to be treated as interdependent in a systems framework. In reality, there is little evidence that this is the case; the various R&D efforts within this subsystem can be likened to a patchwork quilt only partially stitched (Lewell 1975). Even though there is a growing deficiency of protein in the world and the need to utilize a greater diversity of aquatic species is recognized, processors are reticent to develop and market new products. Nor are they, or the fishermen, apparently interested in adopting adequate quality control measures. The potential effectiveness of the research effort on new products and on quality control is thus limited.

Over the years, the FMS R&D effort in quality control and new products, process development, and handling techniques provides yet another example of a "bottom-up push" situation. Laboratory directors have encouraged various R&D thrusts over the years and have developed various strategies to stimulate client interest and acceptance. Emphasis has shifted from fairly long-term endeavours to those emphasizing more immediate application, the latter being in current favor (Caissie and Willmer 1976). The response, however, has generally been disappointing. Wherein, then, lies the problem?

It can be assumed that the Department of the Environment recognizes utilization as a significant component of its activities. Certainly, in terms of dollars generated, it equals that of the primary fisheries. Yet, the effort expended on utilization does not approach the effort applied to the primary fishery.[6] The policy of the Department, then, may appear to be predicated on the assumption that the secondary industry is taking full advantage of opportunities available. This does not seem to be the case. Or perhaps a highly innovative and opportunistic industry would result in demands on the primary industry which could not presently be met on a socially and ecologically sound basis? If so, is there not a need to make this explicit? In any case, for research and development activities related to utilization to effectively meet the test of relevance requires, first and foremost, some explicit statement of policy. Policy development activities begun in 1974–75 in the FMS should be accelerated with a view to filling this essential gap.

Let us presume such a policy recognized a departmental responsibility in the spectrum of activities from harvest to consumption noted above — the need for increasing the proportion of present harvests and the range of species to be used for food[7] and the responsibility of government to encourage industry into taking appropriate action. From this would emerge a number of action strategies that would lead to definition of the needs and priorities for research. Given the present lack of explicitly stated policy, is it any wonder that scientists in the field of utilization R&D across the country ask "what does government expect of us in this new 'relevant science' world?". If it's no longer "bottom-up push" where is the "top-down" direction? If an integrated approach to the problem were taken and some systematic order were introduced in the develop-

[6]In 1973 the landed value of the total fish catch was $300 million, the marketed value was $650 million, and the value added was $220 million. In 1974–75 the FMS devoted $34 million and 1700 man-years to programs related to the primary industry and $14 million and 700 man-years to those related to the secondary industry ($6.9 million of this was for a regulatory program).

[7]Recent initiatives to increase markedly the proportion of the herring harvest in the Bay of Fundy for food as opposed to fish meal represents a recent policy posture.

ment of a responsive structure (e.g. as in that of Jantsch as proposed by Pritchard for Aquaculture), research on marketing, institutional arrangements and alternatives, and related social science topics would be required on a continuing basis to complete the requisite R&D picture. As expressed throughout this paper, an applied systems approach would serve to integrate this total knowledge package in a relevance framework. Thus, in addition to the need for a policy, the requisite strategies, institutional arrangements, and methods to provide for an effective link between scientific, marketing, and management endeavours should be developed.

Some steps have indeed been made in this direction. In 1974, for example, a federal-industry meeting was held as part of the priority-setting process (Environment Canada 1974). There is need for continued interaction of this type in an ordered framework involving scientists, operational people, decision-makers, and client groups.

4.4 Aquatic Environmental Quality

A different situation is the complex one of aquatic environmental quality. As a result of the great interest in environmental quality during the second half of the sixties, research in this area was afforded high priority. Since research on environmental quality could be readily justified in a number of different agencies, a bandwagon effect resulted. Since then, efforts to consolidate forces have met with little success; indeed, the momentum of the sixties is still increasing in the agencies concerned and more are getting involved (Hamilton 1976; Harvey 1976). The availability of resulting scientific information justified the development of environmental quality objectives, which in turn justified an increase in scientific effort. This bandwagon effort was evident in the FMS and undoubtedly many ongoing research programs merely continued under a new title that reflected the new priority (Caissie and Willmer 1976). The phenomenon, which is being repeated today in the planning of energy R&D is another example of a "bottom-up push." The dominant force emerged from those who could show that they "have," "know how," and "know what" — the scientists. The questions not yet addressed satisfactorily on a continuing basis are those that deal with overall direction "where ought we be going" and "why." The latter are value questions and answers derived from the knowledge base and technique of the human and social, as well as the natural sciences. The situation today, then, is one in which there is considerable duplication of scientific effort (Harvey 1976). But the real problem lies in the differences, among the various agencies involved, in their perception of the problem and their answer to the "where ought we be going" or "why" questions. To illustrate, the perception among Fisheries and Marine people of "where" and "why" is based on conceptual underpinnings that can briefly be described as: "water quality criteria must take cognizance of the total aquatic system, recognizing the interdependence of the living elements; the indicator of quality is therefore the health of the biological system which might be inferred by the health of a particular species." Other groups, within the same department, stress chemical monitoring — accumulation of data at high cost — which presumably provides a basis for drawing inferences on possible effects. This empirical approach is identified as one-sided in this report (see "Enquiry Systems") and tends to lead to an undue scientific emphasis on the measurement of extremely low concentration of contaminants to the detriment of research on effects. Differences based on such variations in concepts and approaches are naturally reflected in attendant control strategies and instrumentalities. Thus, the science that supports the different groups, while striving for the same objective of improving water quality, conducts its studies within quite different frameworks.

Resolution of the problem of effective use of scientific resources in the area of water quality will require continuing emphasis at the value-policy level. This cannot be accomplished at the strategic level by groups representing the various different perceptions and interests without supportive unbiased policy research in a systematic approach. Here again is an illustration of the need to provide some formal organizational and methodological link between science and the policy–management system. Development of a comprehensive and national policy is critical to the effective use of scientific resources in this field.

4.5 Other Subsystems

There are other areas in which existing institutional arrangements do not readily facilitate development of a relevant science. These include coastal zone and estuarine management and recreation. Such topics have a Fisheries and Marine interest but also involve the interests of other agencies, federal and provincial (Mann 1976a, b; Parsons 1975). While cross-departmental and cross-governmental initiatives are not uncommon in dealing with this class of problem in planning and action frameworks, the supporting scientific activities are, for the most part, limited to data collection and use of existing knowledge. There are spin-offs, of course, since "why" or "how" questions will inevitably be raised which lead to

more basic research activity, too often ad hoc and disciplinary in focus.

In oceanography, a fairly effective mechanism has been developed to overcome this difficulty. The areas of climate prediction, ocean nonrenewable resource development, transport, and defence depend heavily on oceanographic science conducted in the FMS. The Canadian Committee on Oceanography provides a coordinative link among agencies and the scientific community and influences priorities for research and policy development. Also, the recent federal initiative to develop an oceans policy should enhance the orderly development of oceanographic science and the potential for the initiation of systematic links between science and those agencies responsible for management and policy decisions.

There is need to consider appropriate mechanisms to coordinate the growing interest and scientific activity in the areas of coastal and estuarine management and aquatic recreation. Because of the nature of the subject areas, research support must be provided within a comprehensive framework to be effective. Some action has been initiated along these lines, for example, the Man and the Biosphere Program, and an earlier initiative of the Inland Waters Directorate in supporting interdisciplinary water resource research programs at several universities. However, no effective mechanisms exist to foster this type of comprehensive scientific activity either in government, in the private sector, or in the university community. All are required, as argued in Section 6.

4.6 Summary

Within the FMS there is a need to introduce ordered methods for the transfer of scientific knowledge into the operations–policy–management areas. The integral involvement of scientists with operational people, decision-makers, and policy advisors in this transfer process would do much to alleviate the concern among scientists that current institutional changes may weaken science through an undue emphasis on shorter term scientific pursuits. The relevancy of the natural science effort will depend on the relevancy of policy and management decisions. Here, the knowledge of the human and social sciences must be more effectively transferred into the system. Illustrations have been provided to show where the introduction of ordered knowledge transfer techniques — generally referred to as applied systems approaches — would strengthen the links between science and policy–management and facilitate the sensitivity of the latter system to available scientific potential.

In the synthesis of knowledge leading to policy and management decision options, innovation is limited by organizational structures and attendant mandates; ordered or systematic mechanisms for taking advantage of scientifically derived insights are not in place. The very structure of government departments and the apparent necessity to attend to today's problems precludes due attention to innovative research in the policy and institutional areas. If the assumption is correct that we must learn to better use the knowledge derived from science in order to address current problems and recognizing the constraints to this form of innovation within government, then it follows that such innovation must be enhanced by activities of non-government bodies. With the current emphasis on contracting out of R&D activities, the private sector may play an increasingly important role here. This is a matter for separate study, however, and cannot be considered in the present paper. The potential contribution of the university community in this context is significant and is discussed in the following section.

5. The University Community

5.1 An Emerging Role

Few would question the influence of the university community in setting the pattern for the future. In this period of social and economic transition, characterized by widely divergent viewpoints, parts of the Canadian community strive to return to the prosperity and paradigm of the fifties and early sixties while other parts search for a new, or conserver, society; some hold to old ways and old institutions while others seek new ways and new institutions, and so forth. There is no doubt that some significant changes are in store. In such times, the traditional role of the university community to educate and to search for new knowledge and new methods might be expected to shift and to focus more attention on exploring new contexts[8] and their possible implications. In light of current knowledge about the way things work, of the interdependency of the many parts — human, social, ecological, technological — new contexts cannot be effectively explored by isolated focus on the parts. This is recognized in resource planning and is reflected by a growing focus on comprehensive approaches to resource and social planning and management. Few would disagree that present attempts at comprehensive planning and management are but first steps. Furthermore, the testing and implementa-

[8]"Context" here refers to the way we look at things as a society and is reflected by our institutions and planning and management modes.

tion of new techniques, such as discussed in the foregoing sections, are fraught with constraints which will be overcome only with time and by new people with new understandings. New people with new understandings are prepared by the university.

5.2 Shifts in Emphasis

There are some indications that governments recognize the need for universities to shift their emphasis in the direction noted and there are indications of a corresponding willingness within the university community to respond. As noted previously, it is the announced intention of the federal government to increase the support of social science research and to encourage interdisciplinary and futures research. Several interdisciplinary research programs at universities have been supported by federal and provincial government agencies during the past decade, including the faltering, but, nevertheless, significant support of the Man and the Biosphere Program by the federal government. Several experimental programs initiated by universities have received provincial government blessing, such as the Faculties of Environmental Studies at York and Waterloo, Environmental Design at Calgary, and the Centre for Resources Development at Guelph.

5.3 Federal Response

To date, however, federal initiatives to support this class of research and hence, training, have been ad hoc, and no federal policy and supporting mechanisms exist. In the Department of Fisheries and the Environment, initiatives to broaden the focus of university support programs have not been successful. With few exceptions, such as the continuing support of the Westwater Research Centre at U.B.C. by the Inland Waters Directorate, university support remains disciplinary or, in a few cases multidisciplinary, in focus.

5.4 The Focus on Discipline

Lest the author be accused of ignoring a continuing need to foster disciplinary research, it is appropriate here to make some observations which again have to do with context. Perry (1968), in an exhaustive study of intellectual and ethical development in the college years, emphasized the close relationship between the knower and the known. Apart from those who are committed to productive revolt, students may imitate the forms of other people's knowledge, but be intellectually and socially sterile. One inference which might be drawn here is that biology graduates (or chemistry, or economic) from different biology (or chemistry, or economics) departments with essentially the same "excellence" rating can be very different in their intellectual response to the real world. In times of rapid change — of changing contexts — an education that has been cast in terms of unwarranted justification of the past or the present will hardly provide the student with the ability to cope in terms of future paradigms, let alone provide leadership.

The need for a student to broaden his understanding of the social, ecological, and physical context in which he might perform is becoming more widely recognized. In recent years there has been an increasing trend for disciplinary departments to expose students "to the language of other disciplines" to other departments and through "interdisciplinary" projects and seminars. The logic that justifies this trend might be stated as follows: (a) recognition that many problems faced today may be related to activities of graduates who have not perceived the broad implications of their scientific or professional pursuits; (b) the need in the face of future uncertainty to prepare students for adaption to changing circumstances in life and in the job market; and (c) recognition that there is a unity in science that has been fogged by disciplinary jargon.

5.5 Education Needs for Science in Resource Management

The foregoing discussion touched on some indicators of change in university roles, in the approach to training and in the perception of science which is supportive of resource management needs. It is useful here to pause and consider the problem from the point of view of the needs for resource management. In discussion of the fisheries and aquatic science systems, evidence was presented to show that there is a gap between those involved in scientific pursuits, and those responsible for operations, resource management, and policy decisions. An approach was proposed to bridge the gap, which, in order to be successful, would demand changes in current perceptions on behalf of all groups involved. In terms of education, the emphasis on context and methodology is in accord with the need prescribed. Also, as noted previously, such emphasis is seen to be highly pertinent to the development of good science and resource managers. Of course, it would be naive to assume that all students could gain a firm footing in pertinent contextual and methodological knowledge, or that all would aspire to become managers. Rather, the point is

that this opportunity should be provided in post-secondary educational programs. Furthermore, the question of whether or not such "broadening" should occur at the bachelors or graduate level is probably not a helpful one. Given the diversity among students, some will tend to be "broad" upon entrance to the university while others at the opposite end of the spectrum, will remain "narrow" throughout life, regardless of exposure (Perry 1968). Perhaps the latter will be weeded out or perhaps they should not be permitted access through more stringent entrance requirements. At the recent Association of Universities and Colleges of Canada Conference (1976), considerable discussion centered around the need to focus more attention on university entrance than upon output and demand aspects.

A graduate program in resource policy and management would seem to be the prime requisite to meet the needs described. Broad concepts (ownership, access, social and ethical aspects, finiteness of resources), methodology (scientific, planning, conflict resolution, impact), and interdisciplinary programs (resource policy and management alternatives) should dominate the research thrust, but in a way to encourage involvement of those with highly specific research interests, whether these be in fisheries, oceanography, forestry, or disciplinary specialities. Professors should be drawn from as wide a variety of faculties and departments as possible rather than building up a large permanent staff. Encouragement should be given for government scientists, planners, and managers to participate. Prerequisites for student entry should not exclude anyone on the basis of undergraduate specialization. The program should be seen as credible, within the university, by governments and the public; the research effort, then, should be focused on real problems and be "plugged-in" to the community through active researcher–client involvement. At the same time, the status quo should continually be questioned through good research and alternatives sought at all levels — policy, strategic and tactical.

A graduate program functioning along the lines noted should have a marked influence on curriculum development at the undergraduate level by virtue of wide professor and student involvement. Indeed, the influence of the program on the undergraduates would be a measure of its success. Appropriate attention to involvement of the community — the clients — should provide the requisite external advocacy to support the program and to ensure absorption of graduates into the job market.

While a number of universities are moving in the direction noted[9] none would currently qualify in terms of these criteria. In part, this is due to the internal and well-known problems associated with tribal instincts and in part because of an inadequate range of requisite undergraduate and/or graduate specialty departments available within a university or willing to become involved. However, there is little doubt that explicit federal, or even departmental, recognition of the need in the form of policy and an accompanying funding mechanism would do much to overcome these and other constraints.

5.6 Enquiry Systems

During the technological age since the second world war, science has been responsive to the demands of a materialistic "widget-oriented" society. A one-sided empiricist approach, where "only collection of data and experiment were considered as "scientific," served this age well" (Boulding 1956). This physical view of "scientific" was adopted by biologists and social scientists and is still held by many in both areas. Indeed, in university training curricula in biology, dominant emphasis is still placed on statistical methodology related to sampling, estimation, and simulation (Regier 1976b). Meanwhile, philosophers (Boulding 1956; Jantsch 1972; Kuhn 1970) and "natural science" philosophers (Gibbons and Voyer 1974; Pritchard 1976; Regier 1976b) and an increasing number of social scientists (Abrams 1965; Chevalier 1969; Foster 1969) call for a broadening of current perceptions of legitimate, or scientific, enquiry that can more adequately address the myriad of social, environmental, and resource problems facing modern societies.

Earlier, it was noted that there are few opportunities in Canadian universities to obtain a good grounding in applied systems methods, particularly as these are pertinent to resource and environmental management. There are signs that the situation is changing. The focus on empiricism and, more recently, on "hard" methods of systems analysis is being complemented by an increasing interest in the general area of enquiry (Gibbons and Voyer 1974; Mitroff and Pondy 1974; Odegard 1971; Regier 1976b). This is reflected in course offerings under various titles — the philosophy of science, the history of science — by

[9]For example, a resource management graduate program is currently being planned at U.B.C. which, if implemented, would come close to meeting the criteria outlined. Similar plans are in progress at the University of Toronto.

nonscience departments. Exposure of students to such courses would seem requisite for developing any in-depth understanding of applied systems analysis in the sense used in this study.

5.7 Summary

It has been argued, then, that there is need for a shift in training and associated research to serve resource management needs. Barriers that exist between scientists and those responsible for operations and resource management and policy decisions are the result of a natural adherence to old paradigms in a changing world. The university, by virtue of its traditional role in education and supportive innovative research, bears a large responsibility in the search for more effective ways of managing our resources. There is need for an increased focus on developing an understanding among students of the context in which they will perform and on enquiry systems which can be used to address the problems faced in resource management. This is seen as a dominant need for training of natural and social scientists and for potential managers. An effective way to accomplish this is to establish a graduate program in resource management designed to facilitate involvement of a wide range of disciplinary interests — professors and students — in a program that focuses on context as well as rigorous scientific enquiry. Some constraints to the initiation of programs of this type are discussed and it is concluded that appropriate federal initiatives could do much to enhance moves being taken in this direction by a number of universities. Some of these initiatives are outlined in the following section.

While this study has focused on university education, it should be recorded that the primary, secondary, and other postsecondary education systems — as well as public information and extension programs — are also victims of the reductionist mode and must gradually change to meet future requirements. But this is another study.

6. Toward a "Relevant" University Support Program

6.1 The Present Situation

Immediately following the formation of the Department of the Environment in 1971, steps were taken to develop a departmental policy on the support of university research (Cartwright and Chevalier 1972). The resulting Subventions Policy was adopted by the Department in 1973. The policy recognized Science Policy trends — emphasis on "relevance," interdisciplinarity, the importance of social science. The university role as one focusing primarily on the development of new concepts was implicit in the policy, and the need to guard against departmental insularity through encouraging liaison was recognized. To effect more control on the conduct of supported research than possible under traditional grants programs, the "research agreement" replaced the outright grant. The concept of mutual benefit to the Department and to the university was inherent in the policy. The policy also enveloped shared facilities and fellowships.

The program has not been an overall success. The reasons for this include the slowness in developing a federal policy on university support, differences of opinion within the Department on the role of the university and consequent departmental–university relationships, the lack of interest in, or understanding of the need for, social science or interdisciplinary research, the tendency to view "relevance" in terms of problems requiring immediate solution, and generally, the low priority given to university support in light of budgetary constraints of the past few years. Budget allocations in the various Service programs have not been critically reviewed and adjusted to reflect priorities for research (e.g. Water Resources Subventions, $1 million; Wildlife, $25,000; Fisheries and Marine, $360,000). Furthermore, in terms of total budgets, the proportion allocated to Subventions is extremely low — $2 million in a total research budget of $192 million in 1975–76.

In 1973–74, the FRB Grants Program was taken over by the Fisheries and Marine Service under the new Subventions Policy. Since, the program had shifted emphasis somewhat. For example, proposal review is currently internal and the program has been nominally expanded to cover a wider range of subject areas, including socioeconomic research. Former block grants to support excellence at a limited number of universities have been phased out (Hays 1968). The budget has decreased in terms of buying power from $360,000 to the purchasing equivalent of $170,000, which has severely limited the program and has not allowed a shift in focus to support new priority areas or interdisciplinary research.

In oceanography, the National Research Council (NRC) has provided development grant support to several university groups (Table 1) with broad guidance from the Canadian Committee on Oceanography (CCO). The Department of Fisheries and the Environment provides ship time for university researchers, which amounted to sup-

TABLE 1. NRC development grants in aquatic sciences ($000).

	Up to 68	68–69	69–70	70–71	71–72	72–73	73–74	74–75	75–76	76–77
Memorial Univ. Ocean Eng.	—	—	—	—	80.0	130.0	149.0	98.0	53.0	—
Memorial Univ. Mar. Sci. Res. Lab.	787.3	100.0	65.0	—	60.0	53.3	120.8	53.3	78.0	80.0
Dalhousie Univ.	—	—	—	—	—	—	214.0	290.0	211.3	136.6
Dalhousie Un. Inst. Oceanogr.	930.0	110.0	89.0	84.0	70.0	62.2	62.2	62.2	59.0	60.5
Dalhousie Univ. Aquatron Facility	—	—	375.0	375.0	250.0	—	—	—	—	—
Huntsman Mar. Lab.	—	—	—	—	75.0	70.0	60.0	45.0	51.2	52.5
GIROQ	—	—	—	—	—	300.0	210.0	250.0	—	—
Univ. of Ottawa	—	—	—	—	—	50.0	101.0	99.0	86.3	80.5
Univ. of Toronto Great Lakes Inst.	550.5	75.0	85.0	85.0	85.0	75.5	75.5	—	—	—
Univ. of B.C.	—	—	—	—	—	—	130.0	102.5	105.8	170.0
Univ. of B.C. Inst. Oceanogr.	930.0	75.0	80.0	60.0	55.0	50.0	50.0	50.0	68.7	70.5
Bamfield Mar. Stn	—	—	—	—	—	—	77.0	42.5	64.0	51.2
Total	3197.8	360.0	694.0	604.0	675.0	791.0	1249.5	1092.5	777.3	701.8

port in the order of $1.2 million in 1975–76 (CCO 1976).

From compilations prepared by Caissie and Willmer (1976), the total federal support through grants and subventions (NRC, FMS, and the Inland Waters Directorate) in areas of general concern to this study is about $5.2 million; of this, less than $200,000, almost all from the Inland Waters Directorate program, is provided for the support of social sciences or interdisciplinary research. While the total federal support is spread over 42 universities, the greatest proportion is centered in seven universities which received in excess of $150,000. These are the universities of B.C., Victoria, Guelph, Toronto, McGill, Dalhousie, and Memorial. The universities of Alberta, Laval, and Quebec (five campuses) received between $100,000 and $150,000 (NRC and DFE). As shown in Table 1, NRC support is also provided to maintain the Huntsman and Bamfield research facilities which are shared by a number of universities.

Other university research is supported under contract and some of this is in the social science area. Also, the Canada Council and other federal agencies (Regional Economic Development, Manpower, Secretary of State, Health and Welfare) support or contract social science research pertinent to the scientific thrust areas described earlier. No data are available to allow an estimate of expenditures from these sources.

6.2 ELEMENTS OF A "RELEVANT" UNIVERSITY POLICY

From the conclusions reached in preceding chapters, it is evident that the present federal support of university research does not conform with the needs for developing a "relevant" science. Firstly, in the natural sciences, while 72% of total NRC support is concentrated in seven universities, only 58 and 50% of total DFE and FMS support, respectively, is provided to the same universities. In times of economic hardship and in terms of developing a "relevant" science, it would appear desirable to focus a greater proportion of the Subventions support in those universities where expertise has been built up and is maintained by the NRC and federal support, generally.

Secondly, the apparent paucity of social science research — certainly, in terms of being integrated into the DFE Subvention Program — parallels the deficiencies within FMS and DFE.

Finally, it follows that the Subvention Program is focused largely on disciplinary research which does not encourage the broader based education discussed in Section 5.

On the positive side, there are 7–10 universities that are in receipt of strong federal support in pertinent natural sciences. These universities are located, for the most part, in the same localities as regional establishments of FMS.

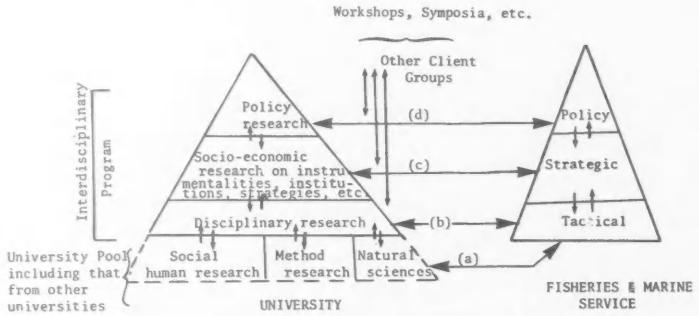


FIG. 8. University–government links.

The University of Manitoba was not included in the 7–10 universities noted above, but obviously should be considered a dominant one in the scheme of things for several reasons. Firstly, the Freshwater Institute is located on campus. Secondly, in terms of NRC and federal support for research in the marine and aquatic sciences it ranks 11th. Thirdly, some precedents have been set in interdisciplinary approaches in the Agassiz Centre and the Centre for Settlement Studies. Finally, the existence of the Resource Management Institute provides added potential for an holistic research approach.

6.3 PRESCRIPTION

A prescriptive model based on the present study can be represented along the lines shown in Fig. 8. Currently, university support through the FMS Subventions Program is dominantly at the tactical level [links (a) and (b)]. Relatively few projects have been supported at the strategic level and none have been funded at the policy level. This does not imply that university researchers have not been involved in fisheries and aquatic science research at the strategic and policy levels. Some research at the strategic and policy levels has been sponsored by the Service under contract; some at the policy level by other agencies such as Canada Council, Regional Economic Expansion, and the Secretary of State. This type of support serves to link individuals in the university with those in government at the various levels shown in Fig. 8. The responsibility for synthesis and use of the knowledge in developing new strategic or policy options rests with the government. However, as mentioned previously, the potential for using knowledge for development of innovative strategy and policy is constrained by the very structure and nature of governments.

By transferring the responsibility for synthesis of knowledge to university groups through support of interdisciplinary research projects, many of these constraints are removed and the potential for innovation is increased. The interdisciplinary approach exposes participating researchers and students to the knowledge base and method of other disciplines, to the synthetic process itself and to the broader contextual areas discussed in Section 5.5. The synergism encouraged through this process adds to the potential for innovation at all levels. Furthermore, evaluation can be accomplished in both a relevance and peer framework. This approach to research, knowledge transfer, and synthesis is compatable with that outlined in Section 4 except that all activities are cast in a research setting. Essentially, this is a unique form of policy research in which hypotheses at the higher levels can be tested against knowledge derived from our understanding of the ecological as well as the human and social systems within an ordered framework. Too often, policy research is conducted by social scientists without the integral involvement of those scientists who understand the biological and physical parameters of the system that will be affected.

To facilitate the research effort and to derive maximum benefit from it, funds should be budgeted for strengthening the links between the research group and the Service at all levels. This might be accomplished by workshops or symposia or through some form of integral involvement of government staff in the research, as illustrated in Fig. 8. Attention should also be given to developing linkages with other client groups such as provincial agencies, industry, unions, and public interest organizations. The establishment of such "learning" links has a number of potential advantages such as increasing the rate of knowledge application and of the development and testing of new insights and the breaking down of institutional barriers. Indeed, university programs could well play an important arbiter role among client groups with disparate interests.

Departmental subvention programs should be

strengthened to enable support of research at those universities that have strong integrated programs in resource management. In light of the current paucity of such programs, a proportion of the FMS and other DFE Subventions resource-oriented programs should be allocated to encourage the development of such programs in key universities, possibly in conjunction with the Man and the Biosphere Program.

Recognizing the need for fostering such research approaches in a time of austerity, various strategies should be considered to get the best returns from the dollar. To this end, cooperation should be sought with other Services and/or departments, provincial agencies, industry with similar or interlocking interests, and the university community itself to foster and cosupport integrated approaches to research. For example, the Department of Fisheries in Nova Scotia, the federal departments of Manpower, Regional Economic Expansion, and the Secretary of State all support social science and/or policy research at Dalhousie University which is directly pertinent to harvest management if considered in the light of optimum sustainable yield. Furthermore, the university is highly supportive of integrated approaches, as is evident by the formation of Environmental and Government Studies Institutes and the plans being formulated to form an Institute of Management that would act as an overall "senate" body for the existing institutes.

Other ways of gaining a multiplier effect from a few dollars include: focus on relatively few universities; close coordination with the NRC and the Canada Council with a view to ensuring the requisite disciplinary backup; integrate the university subventions program with the fellowship program, the career-oriented and special student hiring programs, and the provision of facilities and ship time to foster liaison and contextual understanding at the student and professor level; encourage sabbatical, transfers, development and educational leave for FMS scientists[10] with emphasis on key universities chosen for major support; encourage work transfer or secondment of professors to government from the key universities and encourage contract work at these universities.

6.4 Training for Future Demands

Because of the paucity of information that would permit a detailed examination of the demand for university graduates, Statistics Canada, in cooperation with the Ministry of State for Science and Technology, has recently surveyed 138,000 persons who reported or possessed a university degree in the 1971 Census (Statistics Canada 1974). The survey was essentially a market survey concerned about utilization and supply–demand for university graduates. Certain occupations such as health occupations and engineering showed a relatively high degree of education — occupation correspondence compared with others such as fine arts, math, and physical science which did not. The occupational grouping of agriculture and biology were intermediate in degree of correspondence, showing that graduates in this group were having trouble finding employment in their field of specialization. The connotation here is that an increase in demand for biologists could probably be met from within the existing labor force. The study has shown a need for focusing forecasting attention on those occupations that exhibit a high degree of education–occupation correspondence (i.e. that exhibit a tight market situation on the supply side) such as dentistry, medicine, law, and some fields of engineering.

Such studies, which rely on historical trends to forecast possible future requirements, have some shortcomings. Firstly, if considered linearly by policy-makers, the effect could lead to a series of self-fulfilling prophecies. In the present study, an attempt has been made to show that, in this rapidly changing world, decisions about the future must be based on something more than projection of the status quo (Triste 1969). Secondly, in the current economic climate, there is an increasing tendency for government intervention in university training and research. The university community is responding to this trend and steps have been taken to explore long-term planning needs (Trotter and Carrothers 1974). One of the questions that will need to be addressed as a part of any long-term planning exercise is that of role. Will future needs demand a continuing emphasis on disciplinary training for the job-market? Or will the shift be toward providing a broad education, perhaps centering around in-depth consideration of a specific interest? In the previous section, the needs described in the resource management area appear closer to the latter. This argument will not be settled in the short run, but should not be weighted toward the status quo by focus on demands for training based on forecasts.

By taking this approach to the demand question, it is apparent that justice could not be done to the subject in the present study. However, if only to ensure that future needs for scientifically trained staff are indeed met, government departments would be abrogating their responsibility if they did not encourage a close liaison and con-

[10]A summary of the present situation is provided by Caissie and Willmer (1976).

tinuing dialogue with the university community in areas pertinent to their interests. In DFE, including FMS, relatively ineffective emphasis has been placed on university matters — support, liaison, education.

7. Summary

From the broader reference to global problems, science policy and new perceptions of environment, resource management and science itself, an attempt has been made to narrow the focus and to identify ways and means of developing a more relevant national fisheries and aquatic scientific effort. There is little doubt that the science conducted within and for operating departments of government must be linked more closely with operations and the policy and management decision process. Within the FMS steps have been taken toward this end by changes in organizational arrangements. It is argued in many quarters that such changes, which link scientists more closely with operational activities, may act to the detriment of much needed longer term research activities. Recognizing that existing planning, management, and administrative procedures reflect a shortterm focus and constrain activities devoted to the longer term, steps are prescribed to reduce these constraints.

It is asserted in this report that the introduction of systematic approaches that involve scientific staff in operational, management, and policy decisions would enhance the flow of scientific knowledge into the decision process. Such approaches should also enhance the sensitivity of the system to the potential of scientists and of the knowledge they command. Thus, in addition to close organizational linkages between scientists and operational and planning groups, a methodological link is required. The techniques broadly described as applied systems analysis are considered pertinent and examples are provided to illustrate where such techniques might profitably be applied and tested.

The introduction of systematic approaches would facilitate the evolution of holistic policy and strategy development — a need that reflects current perceptions of the nature of resource and environmental problems. Here, however, additional problems must be dealt with — how to better utilize the knowledge base of the human and social sciences.

If the argument is valid that we must find ways of dealing with resource and environmental problems more holistically, then the effectiveness of the natural science effort will depend heavily on the effectiveness of the translation of human and social science knowledge into the policy and strategy areas. In government, innovation in human and social science research is limited by the structural bounds within which it must operate.

To overcome this problem, in the short term through research and in the long term through education, a case is made for developing more effective links between the university community and governments. The freedom to innovate has long been a prime forté of the university. It is argued therefore, that interdisciplinary research programs in universities that focus on the integration of knowledge toward policy-level objectives and involve the requisite disciplines of the human, social, and natural sciences, could enhance innovation at all levels in government — policy, strategic and tactical. The implications of such comprehensive research activities on education are discussed. Future demands for education, based on the emerging perceptions of current problems, point to a need for a deeper understanding among graduates of the context in which they will work and of the range of enquiry systems that may be employed.

The prescription for a relevant university support policy is integrally related to the prescription for a relevant science program within the FMS. University programs designed to innovate at all levels — policy, strategy and tactics — and linked closely with FMS and other clients and customers, including industry, must serve a key role in creating a more relevant national fisheries and aquatic science effort. The framework for a relevant scientific program discussed in this paper is conceptually represented in Fig. 9. Essentially, it is a network of interests set in a learning context that both serves and extends beyond a single departmental mandate to facilitate the exploration of problems in a comprehensive fashion. The various initiatives identified herein are complimentary; hence, action should focus on all fronts simultaneously. In certain areas, initiatives have already been taken, in others precedents have been set and in others trends are being established, for example:

a) organizational changes in FMS are compatable with the framework for a relevant science;

b) the concept of fisheries management is rapidly changing from that of a "free access–common property resource" to one of stewardship that recognizes the interdependency of human, social, ecological, and economic parameters;

c) several recent initiatives are evidence of a recognition of the need to find ways and means of dealing with resource problems in a more holistic way, for example, (i) the growing interest in and use of systems approaches and the extension of the ecological models to include social and economic parameters, (ii) the interest in and government

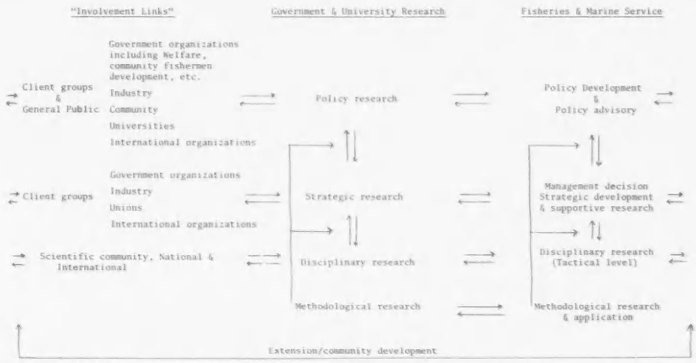


FIG. 9. Framework for "relevant" fisheries and aquatic science.

support of the Man and the Biosphere Program, (iii) precedents within FMS to link, in an ordered way, various interests to enhance the decision and policy process, and (iv) the Canada Water Act and the associated initiatives of the former National Advisory Committee on Water Resources Research to establish several inter- and multidisciplinary water resource research centers at Canadian universities;

d) experimentation within the university community with new pedagogic and research approaches and growing interest in methods of enquiry that focus on integration of knowledge and the growing recognition and support of such initiatives by governments;

e) renewed efforts by governments to rationalize the financing of university research and within universities, an increasing focus on the role of the university; and

f) policy initiatives in the areas of fisheries management, extended jurisdiction including Canada's participation in the Law of the Sea Conference and in the development of an oceans policy.

The foregoing provide a basis for developing a relevant national program in fisheries and aquatic science. Steps required to enhance progress and that are developed in terms of possible action in this paper include:

a) explicit science policy recognition of an ecological objective for scientific research;

b) encouragement of interdisciplinary research and education in universities;

c) development of national policies in the areas of aquaculture, utilization, aquatic environmental quality, coastal zone, estuarine, and lake management;

d) introduction of systems approaches to facilitate the ordered translation and transfer of knowledge into the policy and strategic areas; and

e) development of a university-related program to strengthen the Service links with the university community and with other clients of university research programs.

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BOOK REVIEWS/COMPTES RENDUS

Diseases of Marine Aquarium Fishes. *M. P. Dulin. T. F. H. Publications Inc. Ltd., Neptune, 1976. 128 p. $4.95.*

I enjoyed reading this clearly written and unpretentious book replete with sensible advice and practical information. The author has organized and presented his material effectively, and it is on this basis rather than on originality of content that the book should be judged. My main concern is whether or not most of the information might not be readily available in a number of books on setting up and maintaining a marine aquarium. Not having been able to read the T. F. H. or other books in a similar vein I can only hope that my misgivings are unfounded. But taken on its own Dulin's book seems well worth its modest price.

The book is almost free of errors and misprints, a tribute to both author and proofreader. However, there are indeed some criticisms worth noting. I feel that the publisher should be more discriminating in the quality (p. 67, upper photo hopelessly dark) and relevance (p. 47 parasites of freshwater fish; p. 71, lower photo seems only a "filler") of the photographs. The anatomic illustrations are unnecessarily crude and they could well have been complemented by photographs of typical fish with the body cavity opened and parts identified, and by a brief outline of pertinent aspects of physiology. It would also have been helpful to have given a rough quantitative guide as to what constitutes overcrowding in mass of fish per gallon and in terms of water quality parameters such as ammonia and nitrite. Incidentally, it seems unnecessarily expensive to use sterile USP ascorbic acid to correct nitrite toxicity when the commonly available tablets would suffice. Further, on p. 60 and 73 the author has incorrectly used the term "hydrostatic pressure" when he is referring to osmotic pressure and "epidemiology" and "endemic" (p. 33), terms based on "demos" (people), rather than epizootiology and enzootic, respectively, when referring to disease in animal populations other than man. But perhaps the most perplexing feature of the book is the inclusion of *Saprolegnia* as an agent of disease of fishes in marine aquaria when the commonly used cure for the fungus disease "saprolegniasis" is a salt bath such as sea water.

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The dermatology of teleost fishes: a bibliography. *J. P. Hatton, R. J. Roberts, and A. M. Bullock. Published by the Library of the University of Stirling, Stirling, Scotland. ISBN 0 901636 11 8. 1967. 264 p. £4.25 (about $8.00) postpaid.*

The senior author, J. P. Hatton, is a science librarian at the University of Sterling, R. J. Roberts is director of the Laboratory of Aquatic Pathobiology, and A. M. Bullock is from the Scottish Marine Laboratory at Oban. Dr Roberts has a longstanding interest in dermatology and dermatopathology of fishes and undoubtedly was the initiator of this worthwhile achievement.

The bibliography contains 1853 references and the author index. References are divided into 10 sections such as histology of the integument, scales, external organs, lateral line, electric organs, pigmentation, bioluminescence, mucus, toxigenesis, and disease. The disease section is further subdivided into inflammation; degeneration and wound healing; dermatopathies caused by bacteria, fungi, parasites, and viruses; neoplasia; nutritional and developmental anomalies; dermatopathies of indefinite etiology; and zoonoses.

Dermatology, and particularly dermatopathology, cannot be sharply separated from general pathology of fishes. Therefore, the authors had to make arbitrary decisions in selection of references to be included or excluded. For this reason, it is not possible to say if some references were not listed because they were not considered as related to the subject. Nevertheless, this bibliography is a worthwhile and highly commendable contribution to histology and pathology of fishes.

Random checking some items between the index and references did not disclose errors. However, reference 1762 has the wrong author, title, and page numbers. In the section on mycotic disease, an important reference by N. Tintigner-Nolard 1973 is not listed.

The shortest is the subsection J 10 "Zoonoses" in which references on zoonoses caused by *Aeromonas hydrophila*, *Erisipelothrix*, other cases of human mycobacterioses, and human infections with helminths are not listed.

Nevertheless, the value of this bibliography far outweighs the few shortcomings that were noticed. It is highly recommended to fish pathologists, comparative pathologists, and a wide range of biologists.

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Books Received/Livres Reçus

October 1976

Aquatic Applications of Ozone. *Edited by Walter J. Blogoslawski and Rip G. Rice. International Ozone Institute, Inc., Syracuse, N.Y. 1975. vii + 226 p.*
(Active and recent research on the use of ozone to solve problems of aquaculture, sewage treatment, and biofouling of power plant and industrial cooling waters is reported.)

Acquaculture Practices in Taiwan. *T. P. Chen. Fishing News Books Ltd, Farnham, Surrey, 1976. xiii + 161 p. £5.00.*
(The culture of 29 species of animals and one species of plant is described for an area where mean monthly air temperatures range from 16 to 28°C.)

Effects of Pollutants on Aquatic Organisms. *Edited by A. P. M. Lockwood. MacMillan Company of Canada, Toronto, Ont., 1976. x + 193 p. $7.50.*
(Nine lectures by exponents of the experimental approach to pollution, given under the auspices of the Society for Experimental Biology, are published in this volume.)

Fishes of the World. *J. S. Nelson. John Wiley and Sons, Inc., New York, N.Y., 1976. xiii + 416 p. $24.00*
(A detailed modern classification of all major fish families and higher groups.)

Fishing with Light. *Ben Yami. Fishing News Books Ltd., Farnham, Surrey, 1976. x + 121 p. £3.75.*
(An FAO manual on methods ranging from primitive to modern methods and tactics.)

Progress in Oceanography. *Edited by Mary Swallow. Pergamon Press, Ltd., Oxford, 1976. Vol. 7. $35.00/yr.*
(Papers now appear as single parts of a volume. This editorial policy is similar to that recently adopted by the American Geophysical Union's Antarctic Research Series.)

Water Pollution – Causes and Cures. *Stephen D. Morton. Mimir Publishers Inc., Madison, Wis., 1976. 151 p. $9.95.*
(This is a book for the layman.)

November 1976

Diseases of Marine Aquarium Fishes. *Mark P. Dulin. T. F. H. Publications, Inc., Neptune, N.J., 1976. 128 p. $4.95.*
(An illustrated manual for hobbyists and fish culturists.)

Environmental Biology of Fishes. *Edited by Eugene K. Balon. Dr. W. Junk B.V. Publishers, 1976. Vol. 1(1). 112 p.*
(This is a new journal that proposes to use a less formal approach to scientific publishing.)

Environmental Toxicity of Aquatic Radionuclides: Models and Mechanisms. *Edited by Morton W. Miller and J. Newell Stannard. Ann Arbor Science Publishers, Inc., Ann Arbor, Mich., 1976. xv + 333 p. $26.50.*
(This book is the Proceedings of the Eighth Rochester International Conference on Environmental Toxicity which addressed itself to a variety of biological, ecological, and regulatory topics.)

The Health of the Oceans. *Edward D. Goldberg. UNESCO Press, Paris, 1976. 172 p.*
(This report prepared for the Intergovernmental Oceanographic Commission will be the starting point for a continuing review of the health of the oceans.)

An Indexed Bibliography of the Striped Bass, *Morone saxatilis* 1670–1976. *Larry O. Horseman and Ronnie J. Kernehan. Ichthyological Associates, Inc., Middletown, Del., 1976. xi + 118 p. $2.00.*
(There are 1505 entries divided into 20 categories.)

Inland Fishes of California. *Peter B. Moyle. University of California Press, Berkeley, Los Angeles, Calif., 1976. viii + 405 p. $20.00.*
(Overview chapters on distribution, ecology, and historic change are provided in addition to details on keys, identification, life history, and status of each species.)

Proceedings of the First International Conference on Aquaculture Nutrition. *Edited by Kent S. Price Jr., William N. Shaw, and Karin S. Danberg. College of Marine Studies, University of Delaware, Newark, Del. 1976. vii + 323 p. $3.00.*
(General nutrition, fish, molluscan, and crustacean nutrition studies were considered by North American, European, and Japanese scientists.)

Errata

Bulletin of the Fisheries Research Board of Canada 191 (1975)

COMPUTATION AND INTERPRETATION OF BIOLOGICAL STATISTICS OF FISH POPULATIONS

by
W. E. Ricker

PAGE 164, line 1 of paragraph 2 should begin: "In situation 1 above, ..."
line 1 of paragraph 3 should begin: "In situation 2, ..."

PAGE 194, line 2. Read "It" instead of "If".

PAGE 196, paragraph 1, last line. Read "column 5" instead of "column 4".

PAGE 198. Add to the legend of Table 8.7:
"The unit of time is 2 months for M and F in the heading, and is 1 year for the F values opposite the calendar years shown at left."

PAGE 202, last line. Read "$F' = M' = 280$" instead of "$F = M = 280$".

PAGE 212, 3rd line from bottom: Read "63.896^2" instead of "63.986^2"

PAGE 214, line 4: Read "0.02621" instead of "0.025690"
line 5: The expression in parentheses should be:

$$= \left[\frac{0.95184 - (0.25723)^2/0.07201}{50 - 2}\right]^{\frac{1}{2}}$$

lines 6 and 14: Read "0.0977" instead of "0.09573"
line 7: The expression in parentheses should be:
$= 0.02621/[0.07201]^{1/2}$

PAGE 232. The 6 lines following expression (9.25) should read:
"where w is weight at time t, measured from a conventional zero at the time the fish would have had weight w_0; Gg is the instantaneous rate of growth when $t = 0$ and $w = w_0$; g is the instantaneous rate of decrease of the instantaneous rate of growth, and also the instantaneous rate of growth itself at the inflexion point of the curve. Expression (9.25) is S-shaped, with an upper asymptote at w_0e^G when t is indefinitely large, and a lower asymptote at $w = 0$ when $t \to -\infty$. The inflexion point is $1/2.718 = 0.368$ of the vertical distance from the lower to the upper asymptote."

PAGE 244, paragraph 4, line 3. Read "column 2" instead of "column 3."

PAGE 259, second line of legend of Fig. 10.4. Read "(F)" instead of "(f)".

PAGE 290, line 3 should read: "Solving this by trial gives $P_s/P_r = 0.400$, $P_r = 1607$ thousand lb, $P_s = 642$ thousand"

PAGE 300, last line of paragraph 3: Read "a" instead of "α".

PAGE 314, third line from the bottom. Read:

$$\text{"}\log_e\left(\frac{250{,}000}{100{,}000} - 1\right) = 0.667t_0\text{"}$$

PAGE 316, Example 13.4. The computations of Y_s and f_s should be written as follows:
"$Y_s = 22.2^2/(4 \times 0.00305) = 40{,}300$ tons
$f_s = 22.2/(2 \times 0.00305) = 3640$ days"

PAGE 323. In the denominator of the left side of expression (13.24) read $\bar{U}_i$ instead of $\bar{U}$. In expressions (13.25) and (13.26), and in the line of text following (13.25), read B_∞^{m-1} instead of B_∞, in all cases. Delete the last paragraph on the page and substitute:
"Like (13.3), the curve described by expression (13.25) begins at the origin ($\bar{B} = 0$, $Y_E = 0$), rises to a maximum, and falls again to the abscissa at ($\bar{B} = B_\infty$, $Y_E = 0$); see Pella and Tomlinson's Figure 1."

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Repeat homing of brown trout (*Salmo trutta*) in Lake Eucumbene, New South Wales, Australia
R. D. J. Tilzey

Circulation and temperature structure in large marine enclosures
J. H. Steele, D. M. Farmer, and E. W. Henderson

A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters **P. B. Bayley**

Distribution, abundance, and resource utilization of littoral zone fishes in response to nutrient/production gradient in Lake Memphremagog **D. Gascon and W. C. Leggett**

A leukocytolytic factor isolated from cultures of *Aeromonas salmonicida*
D. W. Fuller, K. S. Pilcher, and J. L. Fryer

A simple mechanism that causes collapsing stability regions in exploited salmonid populations **R. M. Peterman**

Uptake and clearance of petroleum hydrocarbons in the ringed seal, *Phoca hispida*
F. R. Engelhardt, J. R. Geraci, and T. G. Smith

Evaluation of tests with early life stages of fish for predicting long-term toxicity **J. M. McKim**

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R. Walker and S. W. Sherburne

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Population differences in the rainbow smelt, *Osmerus mordax*: multivariate analysis of mensural and meristic data **D. G. Copeman**

Intertidal kelp response to seasonal environmental changes in a British Columbia inlet
L. D. Druehl and S. I. C. Hsiao

Response of the crayfish *Orconectes virilis* to exploitation **W. T. Momot and H. Gowing**

Analysis of zooplankton population fluctuations in the Strait of Georgia, British Columbia **G. A. Gardner**

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Thyroid activity of alewives (*Alosa pseudoharengus*) and rainbow smelts (*Osmerus mordax*) in the Great Lakes **R. Sonstegard, J. F. Leatherland, and R. Moccia**

A multiple opening and closing plankton sampler based on the MOCNESS and N.I.O. nets
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Book Reviews/Comptes rendus: Water resources of the world. Selected statistics (Fritz van der Leeden), **C. J. Low**; Encyclopaedic dictionary of mathematics for engineers and applied scientists (I. N. Sneddon [ed.]), **D. Farmer**; Zooplankton fixation and preservation (H. F. Steedman [ed.]), **C. J. Low**; An illustrated key to freshwater and soil amoebae (F. C. Page) **C. J. Low**

ANNOUNCEMENTS / AVIS

First Quebec Conference on Remote Sensing

Invitation to Submit Communications

The first conference of l'Association québécoise de télédétection will be held in Montreal, November 3 and 4, 1977, to study and review the most appropriate means and resources (human, technical, institutional, etc.) of integrating remote sensing with natural resource management in Quebec.

The conference will devote ½ day to each of the themes: water, soil, and vegetation. Two guest speakers will address each theme, one from the viewpoint of management, the other on the scientific and technical aspects of remote sensing. A series of communications (10–15 minutes each) will follow, illustrating use of the technique in the inventory, development, and supervision of a resource. A round table discussion will conclude each theme.

For further information contact

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Le Premier Congrès Québécois sur la Télédétection

Invitation à Soumettre des Communications

Le premier congrés de l'Association québécoise de télédétection se tiendra à Montréal les 3 et 4 novembre 1977. L'objectif premier de cet évènement scientifique est l'étude et la discussion des moyens et des ressources conséquentes (humaines, techniques, institutionnelles, etc.) les plus appropriés permettant d'intégrer adéquatement la télédétection à la gestion des ressources naturelles au Québec.

Les activités du congrès seront regroupées autour des thémes suivants: l'eau, le sol et la végétation. Au début de chaque demi-journée, consacrée à l'étude d'un thème particulier, deux conférenciers invités traiteront, l'un de l'aspect gestion, et l'autre des aspects scientifiques et techniques de la télédétection. Suivra une série de communications (de 10 à 15 minutes chacune) qui illustreront l'utilisation de cette technique dans l'inventaire, l'aménagement et la surveillance de l'une ou l'autre ressource. Enfin, une table ronde complètera le dossier consacré à chacun des thèmes.

Pour plus de renseignements veuillez communiquer avec:

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Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

JFRBAK34(7)887–1078(1977)

ISSN 0015-296X

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